ZOFIA KIELAN-JAWOROWSKA

EVOLUTION OF THE THERIAN MAMMALS IN THE LATE CRETACEOUS OF ASIA
PART I. DELTATHERIDIIDAE

(Plates XXVIII-XXXV)

Abstract. — A Late Cretaceous mammalian family of metatherian-eutherian grade from Mongolia, the Deltatheridiidae, is described. It contains two monotypic genera: *Deltatheridium* and *Deltatheroides*. A mandible of *Deltatheroides cretacicus* GREGORY & SIMPSON from the Djadokhta Formation is described for the first time. Two subspecies of *Deltatheridium pretrituberculare* GREGORY & SIMPSON are recognized: the nominal subspecies from the Djadokhta Formation and *Deltatheridium pretrituberculare tardum* subsp. n. from the younger Barun Goyot Formation and Khermeen Tsav formation. *Deltatheroides cretacicus, Deltatheridium pretrituberculare pretrituberculare* and *Deltatheridium pretrituberculare tardum* form a morphological sequence, *Deltatheroïdes* being the most primitive. The snout of *Deltatheridium* shows resemblance to primitive marsupials, however, the points of resemblance are primitive features. Dental formula of the Deltatheridiidae is $\frac{?4\ 1\ 3\ 4\text{-}3}{1\text{-}2\ 1\ 3\ 4}$. The shearing surfaces of the molars of *Deltatheridium* are discussed and it is shown that both surfaces 1 and 2 (CROMPTON, 1971) were present, with surface 2 slightly larger. The Deltatheridiidae are very different from the known eutherian mammals of the same age of Asia. They probably derive from the Early Cretaceous Aegialodontidae. The forms closely related to the Deltatheridiidae appear to be the Pappotheridiidae from the Albian of Texas. *Potamotelses* from the Early Campanian of Alberta, classified as a therian incertae sedis, is not related to the Deltatheridiidae. The Late Cretaceous metatherian family Stagodontidae shows some resemblance to the Deltatheridiidae but it is possible that the similarities between the two families are due to the convergence. The Deltatheridiidae cannot be placed with confidence in either Eutheria or Metatheria (in spite of their metatherian dental formula); if they prove to be metatherians, they will constitute a specialised-aberrant group. In this paper they are simply classified as a primitive group of therian mammals. The descendants of the Deltatheridiidae are not known.

Contents

INTRODUCTION

GREGORY and SIMPSON (1926) erected the family Deltatheridiidae, to which they assigned *Deltatheridium*, *Deltatheroides* and tentatively also *Hyotheridium*, all from the Late Cretaceous Djadokhta Formation of Mongolia. The material of all these genera, on which the original description of GREGORY and SIMPSON was based, is housed in the American Museum of Natural History and is scanty and poorly preserved. The poor state of preservation of the teeth in *Deltatheridium* and *Deltatheroides* led GREGORY and SIMPSON to the statement that in the Deltatheridiidae the paracone and metacone are (1926, p. 6): "barely if at all separated or very closely approximated"; this has subsequently been shown (BUTLER & KIELAN-JAWOROWSKA, 1973) not to be the case. The postcanine upper teeth were recognised by GREGORY and SIMPSON in *Deltatheridium* as three premolars and three molars, while in *Deltatheroides* as four premolars and three molars. A comparison of the original specimens with the drawings of GREGORY and SIMPSON (Text-figs 1*A*, *B*) indicates that the only obvious difference between the two genera is the presence in *Deltatheroides* of an additional vestigial upper molar, which is evidently absent in *Deltatheridium*.

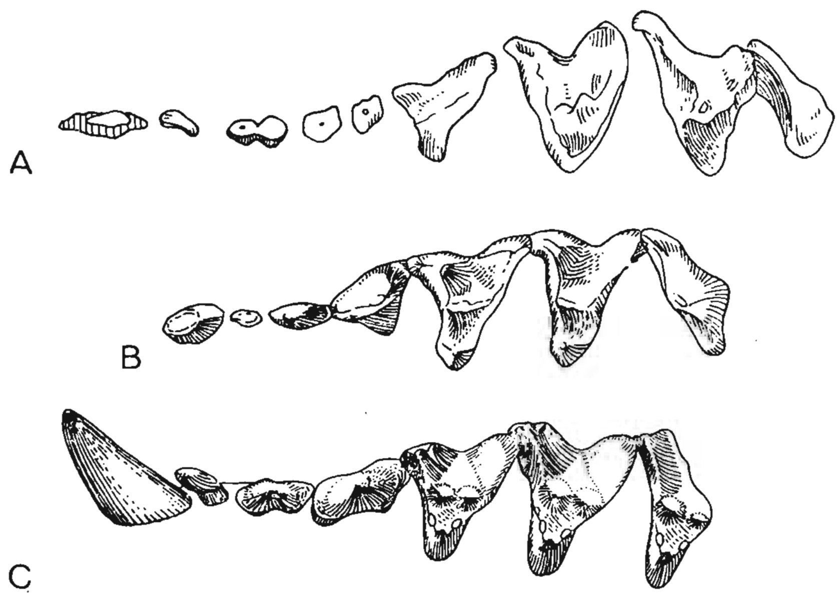


Fig. 1
Comparison of the occlusal views of the upper teeth of *A*, *Deltatheroides*; *B* and *C*, *Deltatheridium*. *A* and *B* are redrawn from GREGORY & SIMPSON (1926), *C* is a reconstruction based on the material of *Deltatheridium pretrituberculare tardum* from the Barun Goyot Formation.

The lower dentition of *Deltatheroides* was not known and is described for the first time in this paper. In *Deltatheroides* there are seven lower postcanine teeth. The postcanine lower dentition of *Deltatheridium* was recognised by GREGORY and SIMPSON (1926) as three premolars and three molars, however, MCKENNA *et al.* (1972) have shown that in the type specimen of *Deltatheridium pretrituberculare* there are also seven lower postcanine teeth. GREGORY and SIMPSON had confused the fourth molar with an enlarged talonid of the third molar.

The Deltatheridiidae have been discussed subsequently by various authors, the most important being the paper by VAN VALEN (1966), who erected the new order of mammals the Deltatheridia. VAN VALEN included in the Deltatheridia the Palaeoryctidae, Didymoconidae, Oxyaenidae and Hyaenodontidae and concluded that the family Deltatheridiidae as defined by GREGORY and SIMPSON (1926) was a junior synonym of the Palaeoryctidae. He placed *Deltatheridium* and *Hyotheridium* in a subfamily Deltatheridiinae and *Deltatheroides* in the Didelphodontinae and placed both these subfamilies in the Palaeoryctidae.

MCKENNA *et al.* (1972) and SZALAY and MCKENNA (1971) revised the genus *Deltatheridium.* They included in the Deltatheridiidae *Deltatheridium* and two Mongolian Paleocene genera: *Sarcodon* (= *Opisthopsalis*) and *Hyracolestes* and removed from the Deltatheridiidae *Deltatheroides* and *Hyotheridium.* The dental formula of the Deltatheridiidae has been recognised by SZALAY and MCKENNA (1971) as $\frac{?4\ 1\ 4\ 2}{2\ 1\ 4\ 2}$. SZALAY and MCKENNA (1971) stated in the diagnosis of the Deltatheridiidae that the last premolar is somewhat molariform, while in fact the fourth postcanine teeth both in the upper and lower jaws are in *Deltatheridium* completely molarized and do not differ from subsequent molars.

BUTLER and KIELAN-JAWOROWSKA (1973) have shown that the dental formula of the Deltatheridiidae (to which they assigned only two Late Cretaceous Asian genera *Deltatheriduim* and *Deltatheroides*) is $\frac{?4\ 1\ 3\ 4\text{-}3}{?\ 1\ 3\ \ 4}$, and claimed that it agrees better with basic marsupial formula than with the eutherian formula. In spite of the marsupial dental formula we did not classify the Deltatheridiidae as the marsupials, but as Theria of metatherian-eutherian grade. The same approach is followed in the present paper.

The Cretaceous therian mammals were known from Asia until recently only from the Djadokhta Formation (GREGORY & SIMPSON, 1926; KIELAN-JAWOROWSKA, 1969). The age of the Djadokhta Formation has been estimated on the basis of multituberculates as ?Coniacian or Santonian (KIELAN-JAWOROWSKA, 1970), but on the basis of further studies of multituberculates I now think that it is more probable that the Djadokhta Formation is of Santonian age. In 1970 and 1971 in Asia new Late Cretaceous mammalian fauna was discovered by the Polish-Mongolian Palaeontological Expeditions (KIELAN-JAWOROWSKA & BARSBOLD, 1972) in the Barun Goyot Formation (previously called also Lower Nemegt Beds), the age of which has been estimated as ? Middle Campanian (KIELAN-JAWOROWSKA, 1974) and in its stratigraphic equivalent informally called Khermeen Tsav formation at the localities of Khermeen Tsaw I and Khermeen Tsav II (see KIELAN-JAWOROWSKA, 1975).

In 1969 the Soviet-Mongolian Palaeontological Expedition discovered in the Gobi Desert in the locality of Khovboor a new mammalian fauna of Early Cretaceous (Aptian or Albian) age (TROFIMOV, 1972). In addition to the representatives of the Triconodonta, Symmetrodonta and Multituberculata, this fauna contains true eutherian mammals, which are the presumable ancestors of two Djadokhta Formation genera: *Kennalestes* and *Zalambdalestes.*

The representatives of the Deltatheridiidae have not been reported from the Early Cretaceous of Mongolia (TROFIMOV, 1972, BELIAJEVA *et al.*, 1974). During my visit to the Palaeontological Institute of the USSR Academy of Sciences in Moscow in June of 1974, thanks to the courtesy of Dr. B. A. TROFIMOV I was allowed to examine the collection of Early Cretaceous mammals from Khovboor, housed in this Institute. In this collection I have seen a mandible with two molars (PIN 3101-32), which in my opinion is similar to *Aegialodon* from the Lower Wealden of Great Britain (K. A. KERMACK *et al.*, 1965). This specimen will be described by Dr. B. A. TROFIMOV. Also Dr. D. DASHZEVEG kindly informed me that in the collection from Khovboor, assembled by him in 1964 and housed at the Laboratory of Stratigraphy and Palaeontology, Geological Institute of the Academy of Sciences of the

Mongolian People's Republic in Ulan Bator, there is a single lower molar ? M_2 similar to *Aegialodon*. It seems possible that the Aegialodontidae are the ancestors of the Deltatheridiidae (see p. 118).

The terminology used in the present paper for describing the elements of the tooth structure is that of VAN VALEN (1966) and SZALAY (1969), while the shearing surfaces are described according to terminology introduced by CROMPTON (1971). SZALAY (1969) designated the cingulum extending from the paraconule antero-labially the paracingulum, while he named the ridge on the anterior edge of the paracingulum the preparaconule crista. The paracingulum may extend labially to the parastyle, or it may fade out before reaching the parastyle, as is the case in *Deltatheridium*. In the majority of primitive mammals on the parastylar region there is a groove which extends from the parastyle upwards and inwards, along which the protoconid moves. I shall refer to this as the groove for the protoconid (Text-fig. 2 *A*). If the paracingulum is long and meets the parastyle, the groove for the protoconid crosses the paracingulum. In more mature specimens this groove is extensively worn (Text-fig. 2 *B*).

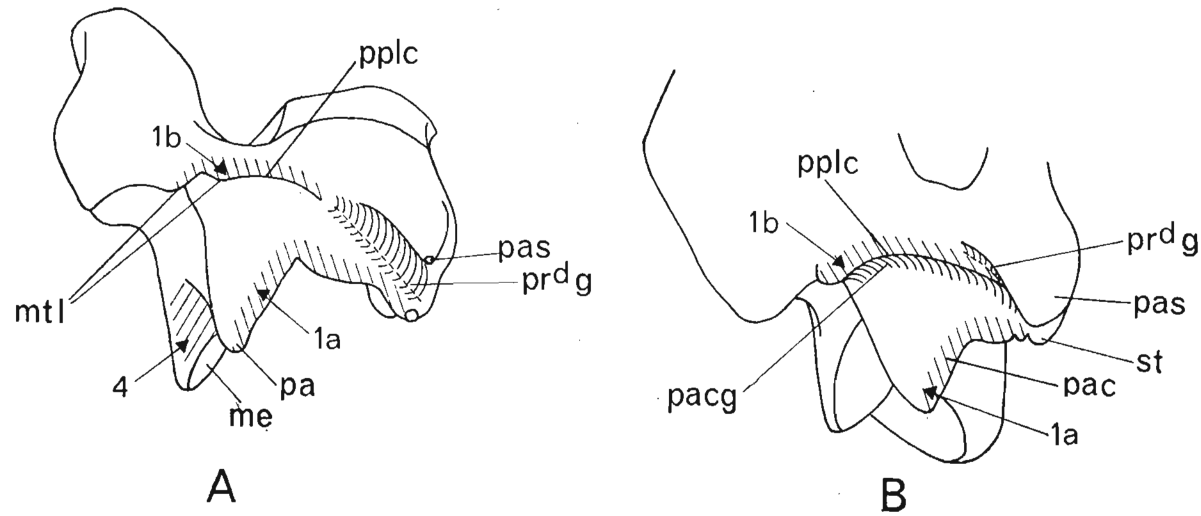


Fig. 2

Comparison of the oblique anterior views of M^2 of *A*, *Deltatheridium pretrituberculare tardum* (ZPAL MgM-I/91) and *B*, M^1 of ? *Gelastops* sp. (MCZ 19734) to illustrate the structure of the groove for the protoconid. Not to scale. For abbreviations see p. 107

The following abbreviations are introduced here to indicate the directions of described elements: long. — longitudinal, parallel to the plane of symmetry of the animal and tr. — transverse, perpendicular and at right angles to the plane of symmetry.

Abbreviations used for institutions:

AMNH — American Museum of Natural History (New York).
MCZ — Museum of Comparative Zoology, Harvard University (Cambridge, USA).
PIN — Palaeontological Institute, USSR Academy of Sciences (Moscow).
SMP-SMU — Shuler Museum of Paleontology, Southern Methodist University (Dallas).
UA — University of Alberta (Edmonton).
ZPAL — Palaeozoological Institute of the Polish Academy of Sciences (Warsaw).

Abbreviations used in figures:

"c"	cusp "c" (CROMPTON, 1971)	pa^d	paraconid
en^d	entoconid	pal	paraconule
hy^d	hypoconid	pas	parastyle
hyl^d	hypoconulid	pplc	preparaconule crista
me	metacone	pr	protocone
me^d	metaconid	pr^d	protoconid
mtl	metaconule	pr^dg	groove for the protoconid
pa	paracone	st	stylocone
pac	paracrista	1*a*, 1*b*-5	matching shearing surfaces
pacg	paracingulum		

ACKNOWLEDGEMENTS

The present paper has been written in part at the Palaeozoological Institute of the Polish Academy of Sciences in Warsaw and completed during my stay in the Museum of Comparative Zoology, as a visiting Alexander Agassiz professor at Harvard University in Cambridge, USA, in 1973-74. I would like to express my deep gratitude to Professor A. W. CROMPTON, Director of the Museum of Comparative Zoology at Harvard, who during my stay in Cambridge has always been willing to both assist me and to discuss questions connected with my work. He kindly read the manuscript of the present paper, and made valuable suggestions. Harvard University provided me with good working facilities during my stay; some of the drawings published in this paper (Text-figs 2, 6, 8) and some of the photographs (Pls XXIX, XXX (partly), XXXI, XXXII and XXXV (partly) were made by Mrs. P. CHAUDHURI and Mrs. A. COLEMAN, respectively, both from the staff of the Museum of Comparative Zoology. The scanning electron microscope photographs were taken by Mr. G. R. PIERCE of Harvard University. The remaining drawings were made by Mrs. K. BUDZYŃSKA, and the photographs by Mr. W. SKARŻYŃSKI both from the Palaeozoological Institute in Warsaw.

I wish also to thank Professor W. A. CLEMENS (University of California, Berkeley), Professor R. C. FOX (University of Alberta, Edmonton), Professor M. C. MCKENNA (American Museum of Natural History, New York), Professor R. H. SLAUGHTER (Southern Methodist University, Dallas), Dr. B. A. TROFIMOV (Palaeontological Institute, USSR Academy of Sciences, Moscow) and Dr. W. D. TURNBULL (Field Museum of Natural History, Chicago) for providing me with the opportunity to study the specimens in their charge. I am also grateful to Professor R. C. FOX and Professor M. C. MCKENNA for reading a part of the manuscript of this paper and their useful comments.

DESCRIPTION OF THE MATERIAL

THERIA OF METATHERIAN-EUTHERIAN GRADE

Family DELTATHERIDIIDAE GREGORY & SIMPSON, 1926

Diagnosis. — Medium sized Cretaceous mammals, length of the skull varying around 4 cm. Snout shortened, nasals strongly expanded posteriorly, contacting the lacrimals. Lacrimals with large facial wing and large lacrimal foramen, strongly resembling that of primitive marsupials, especially *Didelphis*. Jugal deep and long. No palatine fenestra. Dental formula $\frac{?4\ 1\ 3\ 4\text{-}3}{1\text{-}2\ 1\ 3\ \ 4}$. Canines very large, single rooted. P^1 single rooted, P^2 and P^3 double rooted with basal cusps. Premolars not molarized. Stylar shelf of molars very large, with oblique grooves extending from paracrista and metacrista to the middle of the ectoflexus. Parastyle and stylocone large, metastylar area large with one style only. Paracone and metacone placed in the centre of the tooth width (tr.), paracone larger than the metacone. Conules large, convex, but hardly discernible in worn specimens. Paracingulum present but not very wide, disappearing at a level above the tip of the paracone, metacingulum absent. Groove for protoconid not very wide. Precingulum and postcingulum absent. Protocone small, low and pointed in unworn specimens. Lower molars: protoconid tall, metaconid smaller than paraconid, talonid narrow (tr.) and lies behind the lingual part of the trigonid, weak crest extending from apex of metaconid to cristid obliqua.

Included genera: *Deltatheridium* GREGORY & SIMPSON, 1926, and *Deltatheroides* GREGORY & SIMPSON, 1926.

Stratigraphic and geographic range. — Late Cretaceous of Mongolia.

Genus DELTATHERIDIUM GREGORY & SIMPSON, 1926

Type species: *Deltatheridium pretrituberculare* GREGORY & SIMPSON, 1926, the only species known, within which the two subspecies are recognised in this paper: *Deltatheridium pretrituberculare pretrituberculare* GREGORY & SIMPSON, 1926, and *Deltatheridium pretrituberculare tardum* subsp. n.

Generic and specific diagnosis. — Dental formula $\frac{?4\ 1\ 3\ 3}{1\text{-}2\ 1\ 3\ 4}$. Narrow spaces between C-P^1 and P^1-P^2. Conules large, rounded, on M^2 labial to the paraconule a small accessory conule is present on the paracingulum. Deep notch in the metacrista, just labial to the metacone base, smaller one on the paracrista. P_1 very small, with two roots arranged obliquely with respect to the length of the jaw. Carnassial notch present on the paraconid protoconid blade (paracristid) on all the molars. M_4 with double cusped trigonid (metaconid absent) and vestigial talonid [1].

Stratigraphic and geographic range. — Known only from the Djadokhta Formation (locality of Bayn Dzak), from the Barun Goyot Formation (locality of Nemegt), and from the Khermeen Tsav formation, stratigraphic equivalent of the Barun Goyot Formation (locality of Khermeen Tsav II), all in the Gobi Desert, Mongolia.

Deltatheridium pretrituberculare tardum subsp. n.

(Pls XXVIII-XXXIV, XXXV, Fig. 2; Text-fig. 1*B*, *C*, 2*A*, 3, 5, 6, 7*B*, 8 left)

Holotype: ZPAL MgM-I/91, strongly compressed and damaged anterior part of the skull of a young individual, associated with incomplete right and left mandibles. Left C-M^3, right M^1-M^2, left P_2-M_3, right I-M_2 and roots of M_3.

Type horizon and locality: Late Cretaceous (? Middle Campanian), Khermeen Tsav formation, stratigraphic equivalent of the Barun Goyot Formation, Khermeen Tsav II, Gobi Desert, Mongolia.

Derivation of the name: Lat. *tardum*-late, occurring later than the nominal subspecies.

Diagnosis. — Dental formula $\frac{?\ 1\ 3\ 3}{1\ 1\ 3\ 4}$. Differs from the nominal subspecies in having a somewhat shorter skull and only one lower incisor, whereas there are two in *D. pretrituberculare pretrituberculare*.

[1] It appears from the investigation on the development of cheek teeth in some modern marsupials (ARCHER, 1972 that P2 are lost during the ontogenetic development and the premolars retained are P1, P3 and P4. Because there is no data as to which teeth were lost in the ontogeny of the Deltatheridiidae, and as the homology of their teeth with those of the marsupials is not clear, I regard it reasonable to designate the premolars in the Deltatheridiidae in the traditional way, i.e., P1, P2 and P3.

Table 1

Dimensions of *Deltatheroides cretacicus* and two subspecies of *Deltatheridium pretrituberculare* in mm.

Species	*Deltatheroides cretacicus*	*Deltatheridium pretrituberculare pretrituberculare*		*Deltatheridium pretrituberculare tardum*			
Formation	Djadokhta Formation			Khermeen Tsav formation		Barun Goyot Formation	
Locality	Bayn Dzak			Khermeen Tsav II		Nemegt	
Mus. cat. No.	ZPAL	AMNH		ZPAL		ZPAL	
	MgM-I/29	21705	21706	MgM-I/91	MgM-I/102	MgM-I/60	MgM-I/136
Width across upper canines		? 9.5	7.1		7.0		
Width across posterior margins of infraorbital foramen					10.8		
Length of the palatal part of maxilla (suture with premaxilla-transverse suture)					9.5		
Width of the palate across M^1 (between the roots)		? 8.0			6.5		
P^1-P^3 ant.-post.		4.8	4.9	4.3	5.4		
P^4-M^2 ant.-post. (along median cusps)		6.3	6.1	6.4	6.7	7.7	7.7
P^4 ant.-post. tr.				2.5 2.6	2.8 2.8	2.8 3.2	2.8 3.0
M^1 ant.-post. tr.				2.6 3.0	3.0 3.6	3.0 3.7	2.9 3.8
Depth of the lower jaw beneath M_2 (labial)	5.5	? 4.3		3.6			5.5
P_1-M_1 ant.-post.	12.0	?11.0		8.3			
M_1-M_3 ant.-post.				7.5			
P_4 ant.-post. tr.	3.0 1.6			2.1 1.2			2.8 1.3
M_1 ant.-post. ext. tr.	3.3 2.0	? 2.9		2.7 1.5			3.0 1.4
P_3 ant.-post. ext. tr.	2.6 1.4	2.2		1.9 1.1			

Material. — In addition to the type specimen, there are four specimens: ZPAL MgM-I/60, Barun Goyot Formation, Nemegt, Red Monadnocks; strongly damaged rostral part of the skull, with left C, P^1 and P^2 and right P^3-M^3. ZPAL MgM-I/102, Khermeen Tsav formation, Khermeen Tsav II; rostral part of the skull with C-M^3 preserved on both sides. ZPAL MgM-I/113, Barun Goyot Formation, Nemegt, Eastern Sayr; badly damaged fragment of left mandible with M_2-M_4. ZPAL MgM-I/136, Barun Goyot Formation, Nemegt, Eastern Sayr; fragment of right maxilla with M^1-M^3, associated with fragment of the left mandible with roots of M_1, M_2-M_3.

Geographic and stratigraphic range. — Known only from the type horizon, from the locality Khermeen Tsav II and from the Barun Goyot Formation, from the locality of Nemegt, Gobi Desert, Mongolia.

Dimensions. See Table 1.

Description. — *The skull* (Text-fig. 3). On the basis of ZPAL MgM-I/102, which is not distorted, one can state that the snout, which is narrow in the anterior part, widens strongly in the region of P^3. The anterior margin of the orbit is placed opposite the P^3-M^1 embrasure. The dorsal border of the maxilla in lateral view is strongly vaulted, being the highest above P^2. The infraorbital foramen in MgM-I/102 is 1.3 mm long, situated above the anterior part of P^3, surrounded posteriorly by the thickened rim of the maxilla; it is higher than figured by GREGORY and SIMPSON (1926, Fig. 8) in *D. pretrituberculare pretrituberculare.* The infraorbital

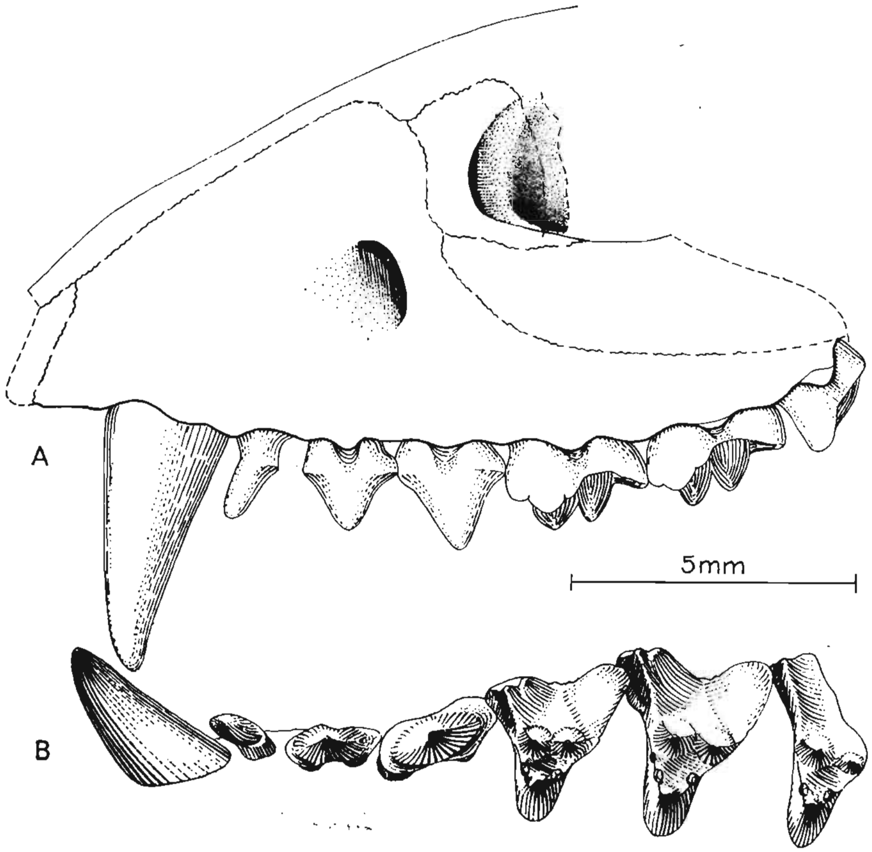


Fig. 3

Deltatheridium pretriturberculare tardum: *A*, (ZPAL MgM-I/102) reconstruction of the anterior part of the skull in lateral view and *B*, reconstruction of the upper dentition of the same species in crown view, based on ZPAL MgM-I/102 and /91.

canal is about 2.7 mm long. The nasals are moderately wide anteriorly, become narrower opposite P^2 and then expand strongly laterally to reach the lacrimals. The naso-frontal suture in studied specimens is not preserved. The lacrimal has a comparatively large exposure on the lateral wall of the face, being somewhat pointed at the anterodorsal corner, between the nasal and maxilla. The lacrimal foramen in MgM-I/102 is 1.1 mm long and is situated in the emargination of the bone, the anterior part of which, i.e., the part in front of the foramen lies more external than the posterior part. The posterior border of the lacrimal within the orbit is not visible, but its ventral border extends posteriorly along the upper and inner parts of the zygomatic arch, as far back as the posterior part of P^4. The jugal extends anteriorly, to the level of the anterior margin of the lacrimal, the distance between its anterior margin and the infraorbital foramen in this specimen is 0.9 mm. In lateral view, above M^1 and M^2 the jugal occupies the upper half of the depth of the zygomatic arch. The zygomatic arch appears to be deeper than reconstructed by GREGORY and SIMPSON (1926, Fig. 8), for *D. pretrituberculare pretrituberculare*.

Palatal region. Palatine fenestra are absent. The palatal surfaces of maxillae are moderately concave. The transverse part of the palatal bone is roughly rectangular, the transverse palatine suture is situated opposite M^1-M^2 embrasure. The anterior palatine foramen is placed in the middle of the length (tr.) on each side of the transverse suture. In front of it a faint palatine groove, which narrows and shallows anteriorly, extends approximately to a position opposite to P^3. Posterior palatine foramina are visible on both sides of MgM-I/102, smaller than the anterior ones and situated just behind them.

Mandible. The mandibles which are preserved in ZPAL MgM-I/91 (young individual) and in MgM-I/136 (fragment), vary strongly in size, but otherwise are similar to those in *D. pretrituberculare pretrituberculare*. The mental foramina cannot be seen.

Dentition. Upper teeth. The examination of the type specimen of *D. pretrituberculare pretrituberculare* (AMNH 21706) confirmed VAN VALEN'S view that there are four alveoli for the incisors preserved on the left side of the specimen, while on the right one only three are discernible, but the first one may not be preserved due to the damage of this part of the premaxilla (Text-fig. 4). The number of incisors in *D. pretrituberculare tardum* cannot be ascertained; as they are not preserved in the studied specimens from ZPAL collections, except for one fragmentary root in front of the canine on the left side of ZPAL MgM-I/102. The canine is large and curved and in ZPAL MgM-I/91 it is 4.8 mm long and in MgM-I/60 is 5.3 mm long. P^1 is small and single-rooted, directed obliquely anteriorly, with a small posterior basal cusp. There is a narrow gap 0.4 mm long in MgM-I/102 between C and P^1, and 0.55 mm long between P^1 and P^2. P^2 and P^3 are double-rooted, transversely compressed, P^2 lower than P^3. P^2 has a small anterior cingulum and comparatively large posterior cusp. P^3 is similar in shape to P^2, but larger and higher. This is the highest of the postcanine teeth. The anterior cingulum is more strongly developed than in P^2, the posterior basal cusp is larger, surrounded by a distinct ridge. The posterior ridge of the main cusp meets the lingual side of the basal cusp.

M^1 is roughly triangular, slightly longer than wide, asymmetrical because of the stronger development of the metastylar region. In labial view M^1 is lower than M^2. The ectoflexus is very deep and the stylar shelf very wide, due to the lingual (central) position of the paracone and metacone. The metastylar region is strongly elongated posterolaterally with a single cusp (metastyle), situated on its postero-lateral corner. The parastylar region is in occlusal view smaller than the metastylar region and three styles: parastyle, stylocone and poorly developed, unnamed style, designated here as style B_1 (BENSLEY, 1906), adhering tightly to the stylocone are present. The latter cannot be designated as a mesostyle (style C) as it is situated in the parastylar region and not in the middle of the ectoflexus as the mesostyle usually is. The stylocone is situated more lingually than the two remaining styles of the parastylar region. Along the middle of the ectoflexus small and indistinct crenulations, visible only on unworn specimens are present. The paracrista and metacrista are developed as very strong ridges. On the metacrista, labially to the base of the metacone there is a deep notch. A similar, but shallower

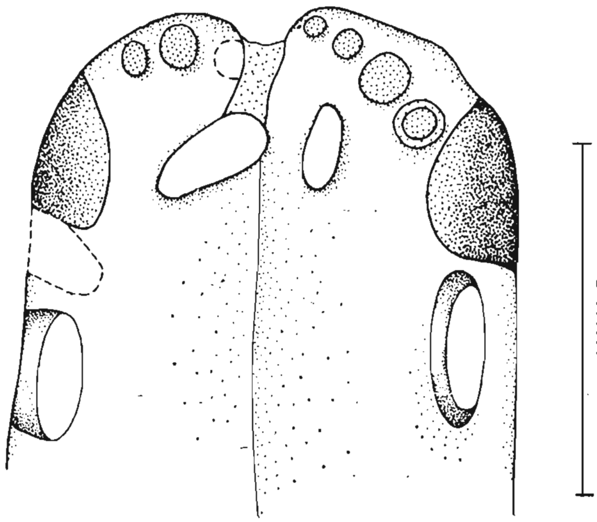


Fig. 4
Deltatheridium pretrituberculare pretrituberculare: (AMNH 21706). Anterior part of the snout in palatal view, showing four alveoli for the incisors on the left side.

notch is present on the paracrista labially to the base of the protocone. Due to the powerful development of the metastylar region, the metacrista is much longer than the paracrista. The stylar area in occlusal view consists of three surfaces: anterior, central and posterior. The central is separated from the anterior and posterior by oblique grooves, which extend from the notches on the paracrista and metacrista to the deepest part of the ectoflexus. The shearing surface above the metacrista is vertical and is not visible in occlusal view. The shearing surface above the paracrista is directed obliquely and can be seen in occlusal view. The paracone and metacone are situated in the middle of the tooth width (tr.), the paracone lies slightly more lingually than the metacone and they have closely approximated bases, but their tips are widely separated. The paracone is higher than the metacone. The conules are comparatively large, swollen cusps, well discernible only in young specimens. The paracingulum extends from the paraconule along the anterior wall of the tooth, it is distinct and fades out at (or slightly beyond) a level above the tip of the paracone. The preparaconule crista is absent. The groove for the protoconid is well developed, widest (long.) in its middle part, disappearing opposite the paracone. A metacingulum is not present. The protocone is small and situated much higher than the paracone and metacone. The precingulum and postcingulum are absent. The lingual part of the tooth is very narrow (long.) in respect to the wide (long.) labial part. The upper anterior and posterior margins of the crown, i.e., the parts in contact with the maxilla, are strongly concave in the middle. In labial view: the parastylar region is large and has a form of a three-lobed petal; the ventral surface of the metastylar region labial to the metacone is strongly concave; the metacone is visible and the paracone is partly obscured by the descending parastylar region.

M^2 is very similar to M^1 but is larger and more symmetrical, the parastylar and metastylar regions are almost equally developed. The paracrista in M^2 in much longer than in M^1. In ZPAL MgM-I/91 on the right M^2, labially to the paraconule, on the paracingulum an extra conule, similar to that in *Pappotherium* is present. On the left M^2 of the same specimen the paracingulum in this region is damaged, while in all other specimens the teeth are worn and the conules are hardly discernible. The incurvature on the crown-maxilla boundary between the roots, along both embrasures, is shallower than in M^1, the paracingulum is poorly developed, but more prominent than in M^1, the groove for the protoconid is wider than in M^1. Otherwise all the details of the structure of M^2 are the same as in M^1.

M^3 is strongly asymmetrical, with a very large parastylar region elongated into a narrow process and the metastylar region hardly developed. The parastylar region is bordered labially by a prominent ridge, and the parastyle and stylocone are hardly discernible. The paracone and metacone are situated in the middle of the tooth width, the paracone being much higher than the metacone. The paracrista is prominent, with a distinct notch, the paracingulum faint and weaker than in M^2. The paraconule is well developed and the metaconule not discernible. The groove for the protoconid is as wide as in M^2. Due to the lack of metastylar region, the metacrista is poorly developed, but the remaining details of the tooth structure are the same as in M^2.

The embrasures between M^1-M^2 and M^2-M^3 are very deep and the maxilla forms a highly domed roof.

Lower teeth (Text-fig. 5). In the right mandible of ZPAL MgM-I/91, in front of the broken canine, the root of a single incisor is present. This incisor was semi-procumbent and oval in outline. The anterior margin of the mandible is preserved, and because there is apparently no space for more than one incisor, it appears that a single lower incisor is characteristic of *D. pretrituberculare tardum.* In other specimens the lower incisors are not preserved. This is the only specimen in which the canine is preserved and its tip is damaged. It is a large tooth, oval in outline and directed vertically and slightly forwards. P_1 was present in the right mandible but was damaged and lost during preparation. It was a very small, cone-like, double-rooted tooth, with roots almost perpendicular to the longitudinal axis of the mandible so that the lingual root lies further anteriorly than the labial. This is a result of the narrow space between C and P_2. A similar condition is present in *Deltatheroides cretacicus* (ZPAL MgM-I/29). P_2 is cone-like, double-rooted (as are all that follow), is much taller than P_1, has a prominent main cusp and a comparatively large posterior basal cusp. The basal cusp (in lateral view) projects posteriorly beyond the base of the posterior root. Along the posterior edge of the main cusp there is a crest, which reaches the middle of the posterior cusp. P_3 is higher than P_2, has a large anterior cusp and a small incipient talonid. The anterior cusp is tall and piercing and wide at the base. On the posterior edge of the anterior cusp there is a crest, which reaches the incipient talonid on the labial side and continues along the length of the talonid as the cristid obliqua, but the latter is directed, in a longitudinal rather than an oblique direction. Labially to the cristid obliqua the talonid slopes downwards, while lingually it is slightly basined. This basined part, placed on the lingual side of the tooth, corresponds to the talonids of M_1-M_3, which in these teeth lie behind the labial parts of trigonids. Cusps on the incipient talonid cannot be recognised.

M_1 is somewhat smaller than M_2 and M_3. The trigonid is larger (long. and tr.) than the talonid, which is distinctly narrower than the trigonid and placed rather lingually. The protoconid is the highest and largest of the trigonid cusps, the metaconid the smallest. The paraconid and metaconid are well separated by a wide furrow. On the anterior edge of the paraconid there is a basal cingulum, directed obliquely downwards. The paraconid and protoconid anterior surfaces form a cutting blade, with a distinct carnassial notch in the centre of the paracristid. On the labial side, the base of the protoconid slightly overhangs the bases of the roots. Posterior wall of the protoconid and metaconid are not vertical but slightly oblique. Along the posterior wall of the metaconid a faint crest (metaconid crest) extends

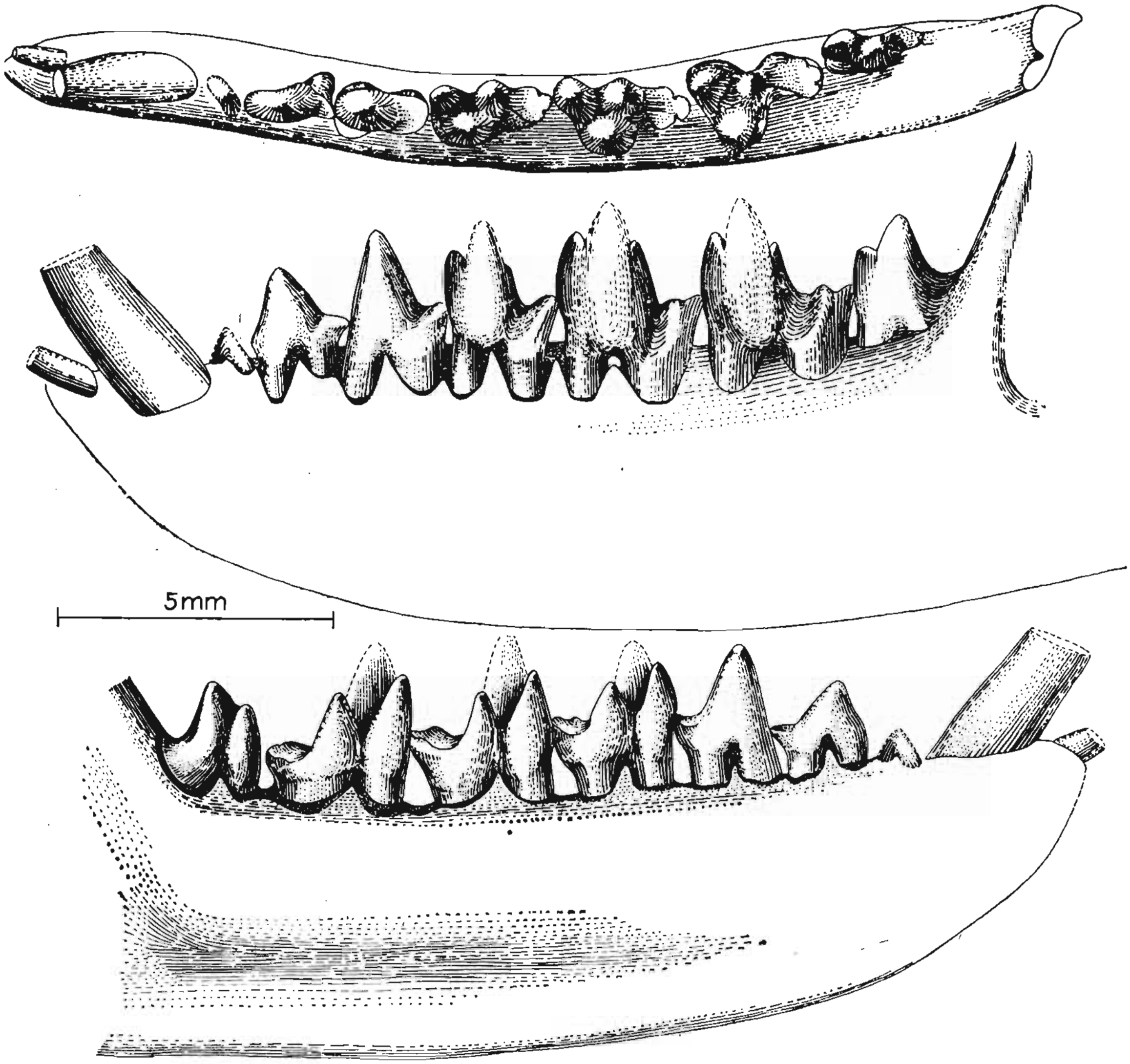


Fig. 5
Deltatheridium pretrituberculare tardus: reconstruction of the mandible and dentition in occlusal, outer and internal views; based on ZPAL MgM-I/91 and MgM-I/136.

from the tip of the metaconid downwards to the cristid obliqua. This crest separates shearing surfaces 1 and 5. The surface of the talonid is in all specimens strongly worn but the three talonid cusps entoconid, hypoconulid and hypoconid can be recognised. A hypoconulid is situated at the very end of the talonid. The hypoconid and entoconid are arranged symmetrically on both sides of the hypoconulid and fairly distant from it. The floor of the talonid basin falls away rapidly on the lingual side and an entocristid is not present. Consequently a well developed talonid basin is not present. The hypoflexid for the reception of the paracone is prominent and shearing surfaces 1 and 3 are well developed. M_2 is the largest of all the cheek teeth, M_4 very strongly reduced. M_2 is similarly shaped as M_1, but differs from it in having more robust protoconid, which projects more strongly labially over the base of the tooth. The metaconid is more strongly separated from the paraconid than in M_1, the prefossid being somewhat larger. The relative size of the talonid is the same as in M_1. The talonid projects beyond the posterior root of the tooth. M_3 differs from M_2 in being slightly smaller and in having the protoconid more robust in relation to the other cusps. M_4 is very small and shorter (both tr. and especially long.) than M_3 and M_2. The trigonid consists of two cusps (protoconid and paraconid), and the metaconid is absent. The protoconid is higher than the paraconid and does not overhang the root labially as in M_3. The talonid is rudimentary and cannot be seen in the labial view, because it is hidden behind the coronoid process. It is narrow, situated lingually and lacks clearly defined cusps.

Variability. — The specimens assigned here to *D. pretrituberculare tardum* differ considerably in size. ZPAL MgM-I/136 is about 1·5 times larger than MgM-I/91 in respect to the depth of the lower jaws. MgM-I/91 belongs to a young individual in which M_3 is just erupting. The differences between these specimens concern not only the size of the bones but also of the lower teeth, which in the larger jaw are on the average about 1.3 times larger than in the smaller specimen. The differences between the upper teeth are less striking, the upper teeth in the specimens MgM-I/136 and/60 are on the average 1·2 times larger than in MgM-I/91, while the specimen MgM-I/102 is intermediate between them. As no differences except the size are observed between the studied specimens and all the details of their tooth structure are identical, I regard all the specimens discussed here as conspecific.

SHEARING SURFACES IN DELTATHERIDIUM

Deltatheridium (Text-fig. 6) has strong shearing along both the anterior and posterior walls of the molars. The anterior walls of the upper molars are oriented obliquely with regard to the median suture. On the anterior wall of the upper molars one can recognise the shearing surface 1a (CROMPTON, 1971). The surface 1b is hardly recognisable because of the poor development of the paracingulum. The paracrista, forming the leading edge of the shearing surface 1a, is a very strong ridge with a distinct but not very deep carnassial notch. The main shearing along the anterior wall of the upper molars was on the surface 1a. On the posterior wall of the trigonid, there is a faint ridge extending from the tip of the metaconid to the cristid obliqua; this separates shearing surfaces 1 and 5. Shearing surface 1 is not divided into two parts as in *Aegialodon*. The posterior wall of the upper molars labial to the metacone is vertical and it forms the strong shearing surface 2, which shears against the paraconid-protoconid blade (paracristid) on the lower molar. On the leading edges of shearing surfaces 2 on both the upper and lower molars there are very deep carnassial notches. The presence of these notches, characteristic for carnassial teeth (see CROMPTON, 1974, Fig. 9) indicates that although in *Deltatheridium* the shearing took place both along the anterior and posterior walls of the molars, shearing surface 2 was slightly larger as in marsupials. This conclusion is supported by study of the type of wear on the paracrista and metacrista in *Deltatheridium*.

The shearing surfaces 3 and 4 on either side of the hypoconid are rather small, 3 somewhat larger than the 4. Matching surfaces are present on the lingual slopes of the paracone and metacone. The protocone is comparatively small and pointed. The talonid is small and lacks a lingual wall, consequently shearing surface 6 is not present. The preprotocrista and post-protocrista do not play an important part in shearing in *Deltatheridium*, whereas the paracrista and metacrista are long and form the leading edges of the main shearing surfaces.

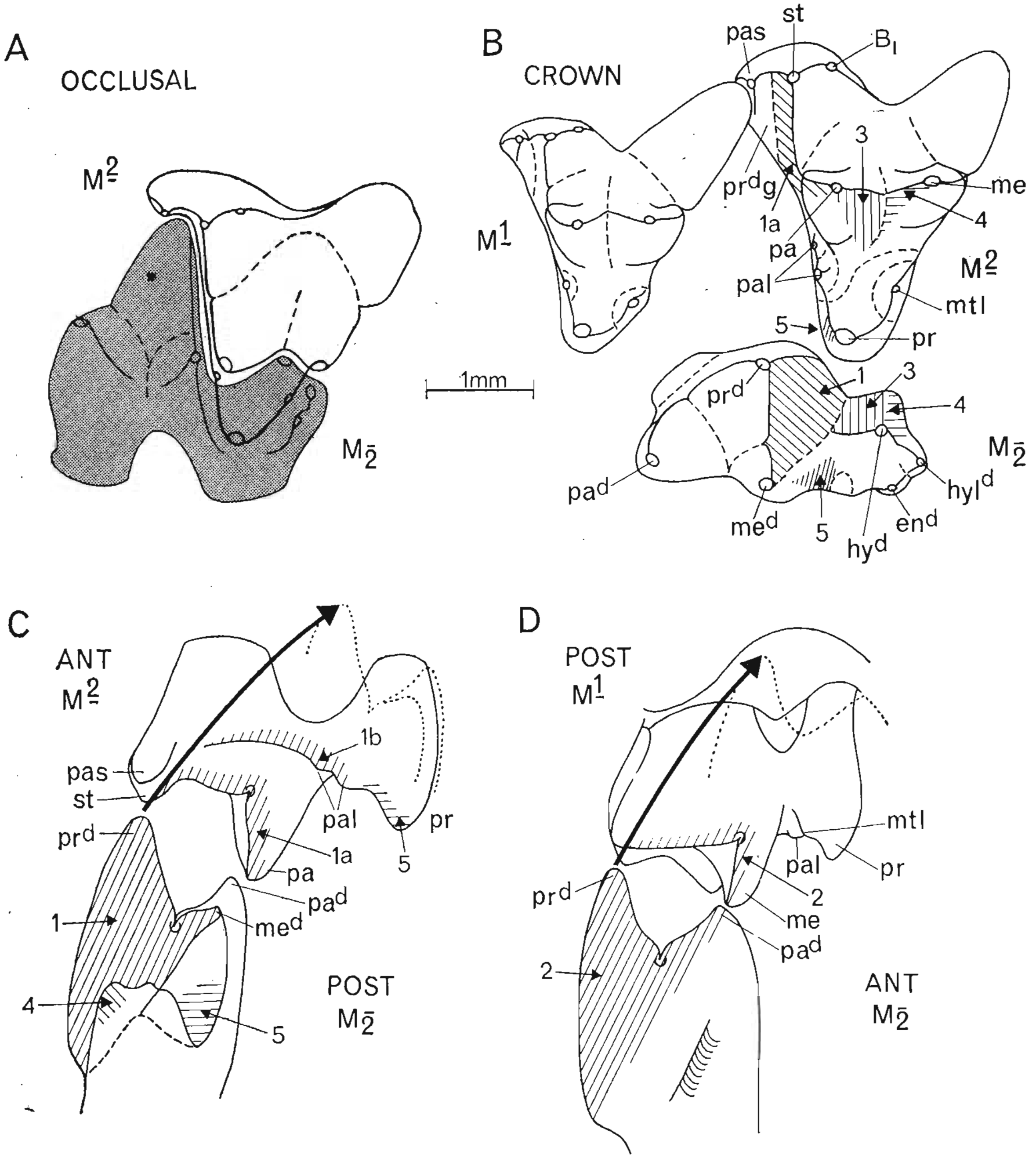


Fig. 6

Diagrammatic drawings of the upper and lower molars of *Deltatheridium pretrituberculate tardum* in four different views to illustrate the shearing surfaces: *A*, occlusal views of M^2 and M_2; *B*, crown views of M^1, M^2 and M_2; *C*, anterior view of M^2 and posterior of M_2; *D*, posterior view of M^1 and anterior view of M_2. The bold arrows on Figs *C* and *D* indicate the direction of movement of the lower teeth against the upper. For abbreviations see p. 107.

Genus DELTATHEROIDES GREGORY & SIMPSON, 1926

Type species: *Deltatheroides cretacicus* GREGORY & SIMPSON, 1926, the only known species of the genus.

Generic and specific diagnosis. — Dental formula $\frac{?\,1\,3\,4}{?\,1\,3\,4}$. Resembles strongly *Deltatheridium* in size, proportions and structure of the dentition. Differs from *Deltatheridium* in presence of vestigial M^4 (absent in *Deltatheridium*) and in the structure of M_4, which has a completely developed trigonid, with metaconid present (absent in *Deltatheridium*) and normally developed talonid (Text-fig. 7).

Stratigraphic and geographic range. — Known only from the Late Cretaceous (?Santonian) Djadokhta Formation of Bayn Dzak, Gobi Desert, Mongolia.

Deltatheroides cretacicus GREGORY & SIMPSON, 1926
(Pl. XXXV, Fig. 1; Text-figs 1*A* and 7*A*)

1926 *Deltatheroides cretacicus* sp.n.; GREGORY & SIMPSON, Pl. 11, Figs 1*c*, 9, 10.

Material. — AMNH 21700 partial face with badly damaged dentition, described and figured by GREGORY and SIMPSON, 1926. ZPAL MgM-I/29 incomplete left mandible with roots of canine and of P_1 and somewhat damaged P_2-M_4. Both specimens are from the Djadokhta Formation of Bayn Dzak.

Dimensions. See Table 1.

Description and discussion. — The upper dentition in the AMNH specimen is strongly damaged and does not merit description. No differences from the upper dentition of *Deltatheridium pretrituberculare* (both subspecies) are observed, except for the presence in *Deltatheroides cretacicus* of vestigial M^4.

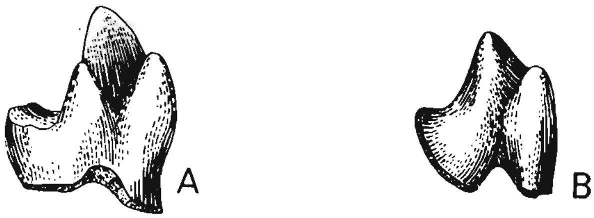


Fig. 7
Comparison of the internal views of M_4 of: *A*, *Deltatheroides cretacicus* and *B*, *Deltatheridium pretrituberculare tardum*, not to scale.

The mandible ZPAL MgM-I/29 found in Bayn Dzak is assigned to *Deltatheroides cretacicus* for the following reasons: the upper molars of *Deltatheridium* and *Deltatheroides* are almost identical and therefore one would expect that the similar lower molars would be present in both genera; the lower molars in ZPAL MgM-I/29 are almost identical to those of *Deltatheridium;* in *Deltatheridium* M^4 is absent, M_4 has a reduced trigonid, without a metaconid and a strongly reduced talonid; in MgM-I/29 M_4 has a three-cusped trigonid and a metaconid which sheared against M^4 (present in *Deltatheroides*); the mandible of ZPAL MgM-I/29 agrees in size with AMNH 21700.

DISCUSSION

EVOLUTION IN THE DELTATHERIDIIDAE

Comparing the teeth structure of *Deltatheroides cretacicus* and two subspecies of *Deltatheridium pretrituberculare* one can demonstrate that the three forms are very closely related. *Deltatheroides cretacicus* and *Deltatheridium pretrituberculare pretrituberculare* are contemporaries, but *Deltatheroides cretacicus* has a structure from which *Deltatheridium pretrituberculare pretrituberculare* could be derived. *Deltatheridium pretrituberculare tardum* was found in younger formation than the two preceeding forms.

In the evolution in this group shortening of the skull took place and this was correlated with the loss of anterior and posterior teeth. The most primitive member of the family is *Deltatheroides cretacicus*, which has four upper and lower molars, M_4 with completely developed trigonid, while M^4 is somewhat reduced. The next in the structural sequence is *Deltatheridium pretrituberculare pretrituberculare* which has two lower incisors (unknown in *Deltatheroides*), and which has lost M^4, while in M_4 the talonid is more reduced than in *Deltatheroides*. The last form in the sequence is *Deltatheridium pretrituberculare tardum* in which there is only one lower incisor, and M_4 is extremely reduced. The trigonid consists of only two cusps (protoconid and paraconid), the metaconid being absent, and the talonid is extremely small and lacks the typical cusps. The details of the structure of M_4 of *Deltatheridium pretrituberculare pretrituberculare* are unknown because in AMNH specimen this tooth is very badly damaged. However, in *Deltatheridium pretrituberculare pretrituberculare* M^4 is absent and one can presume the loss of the metaconid in M_4 in this subspecies, because M_4 sheared only against the metacrista of M^3.

COMPARISON OF THE DELTATHERIDIIDAE WITH OTHER THERIA OF METATHERIAN-EUTHERIAN GRADE

The most primitive known therian mammal is *Aegialodon* represented by a single lower molar from the Lower Wealden of Great Britain (K. A. KERMACK *et al.*, 1965). The forms similar the *Aegialodon* are now known from the Early Cretaceous of Asia, although they have not been described as yet (see p. 105). Also a lower molar from the Albian of Texas, identified as Trinity molar type 6, SMP-SMU 61728 (SLAUGHTER, 1971) is approximately at the same level of organization as *Aegialodon*, although has a slightly longer talonid. All these forms could possibly be placed in the same family the Aegialodontidae. The Aegialodontidae are similar to the Deltatheridiidae in that the paraconid and metaconid are of the same height or the paraconid is slightly larger and both are considerably shorter than the protoconid; the talonid is narrow (bucco-lingually), is lingually placed and lacks a medial wall. However, in the Aegialodontidae the molars are smaller than in the Deltatheridiidae and have a smaller talonid basin, which indicates that in the upper molars the protocone was smaller than in the Deltatheridiidae. A primitive feature of the Aegialodontidae is the presence of both an anterior buccal cingulum and an anterior lingual cusp or ridge. The lingual cusp or ridge is lost in the Deltatheridiidae, although it is retained in some Cretaceous mammals (e.g. in some marsupials). It seems possible that the Aegialodontidae are the ancestors of the Deltatheridiidae.

PATTERSON (1956) described several isolated lower fragmentary upper molars from the

Trinity sandstone (Albian) of Texas, which he classified as Theria of metatherian-eutherian grade. Slaughter (1965) described from the same beds but a different locality last two upper molars which he designated *Pappotherium pattersoni*, and for which he created the family Pappotheriidae within the subclass Theria. In the same paper he described several lower molars from the same beds, without naming them. The Trinity therians have been subsequently described by SLAUGHTER (1968*a*, 1968*b*, 1968*c*, 1971), CROMPTON (1971) and TURNBULL (1971).

The upper molars of *Pappotherium* strongly resemble those of *Deltatheridium* (Text-fig. 8), although *Pappotherium* is much smaller than *Deltatheridium*. The parastylar region has the same form in both genera, the parastyle and the stylocone in both cases are prominent, the difference is that in *Deltatheridium* an extra cusp, closely adhering to the posterior surface of the stylocone is present; this gives the parastylar region in labial view the appearance of a three-lobed petal, while in *Pappotherium* this petal has only two lobes. The groove for the protoconid in *Pappotherium* is wider than in *Deltatheridium*, especially in its most labial part. In both genera the paracingulum does not meet the groove. The ectoflexus is strongly concave in both genera and there are indistinct crenulations along its margin, the mesostyle (stylar cusp C) is not present. The metastylar region is large and strongly elongated postero-labially in *Deltatheridium* and supports a single cusp (metastyle) whereas in *Pappotherium* it is less elongated and supports two cusps.

In both genera on the stylar shelf one can recognise three surfaces, separated by grooves extending from the lingual corners of the paracrista and metacrista towards the middle part of the ectoflexus. On the metacrista in *Pappotherium* a small cusp "c" (CROMPTON, 1971) is present, while in *Deltatheridium* there is a carnassial notch on the metacrista. The paracone and the metacone are similarly shaped, in both genera the paracone being larger and placed more lingually and in both the paracone and the metacone are partially concave on their labial faces. Conules are present in both genera; they may be slightly larger in *Deltatheridium* but in both cases they are not winged (i.e., lack a postparaconule crista). In one M^2 of *Deltatheridium pretrituberculare tardum* an extra conule is present on the paracingulum, labially to the paraconule, as in *Pappotherium*. The groove for the protoconid in *Pappotherium* is wider than in *Deltatheridium*, especially in its labial part. Also, the paracingulum is wider in *Pappotherium* than in *Deltatheridium*, but in both genera it does not meet the groove for the protoconid. The protocone is small and pointed and at a horizontal level considerably higher than the paracone in both genera. The lingual side of the tooth is relatively narrower (long.) in *Deltatheridium* than in *Pappotherium*.

The lower teeth of *Pappotherium* are not known. CROMPTON (1971) has chosen a lower molar SMP-SMU 61726 from the Trinity sandstone as a possible lower molar of *Pappotherium*, while SLAUGHTER (1971) has tentatively assigned a left lower jaw fragment SMP-SMU 61992 to *Pappotherium*. The mandible fragment is according to SLAUGHTER an eutherian because a replacing tooth for the penultimate premolar is preserved. The lower molars chosen by CROMPTON and SLAUGHTER as possibly belonging to *Pappotherium* differ considerably from each other and I think that it is impossible to demonstrate unequivocally that either of them matches the upper molars of *Pappotherium*. The study of the structure of the upper molars of *Pappotherium* and *Deltatheridium* shows that in both genera both shearing surfaces 1 and 2 are used. However, in *Pappotherium* the main shearing was on surface 1, whereas in *Deltatheridium* it was on surface 2. In this respect *Deltatheridium* is somewhat more similar to marsupials than *Pappotherium*. If the relative sizes of the shearing surfaces in *Deltatheridium* and *Pappotherium* described above are correct, one would expect that the lower molars of *Pappotherium* may differ from those of *Deltatheridium*, and the former may have a paraconid smaller than the

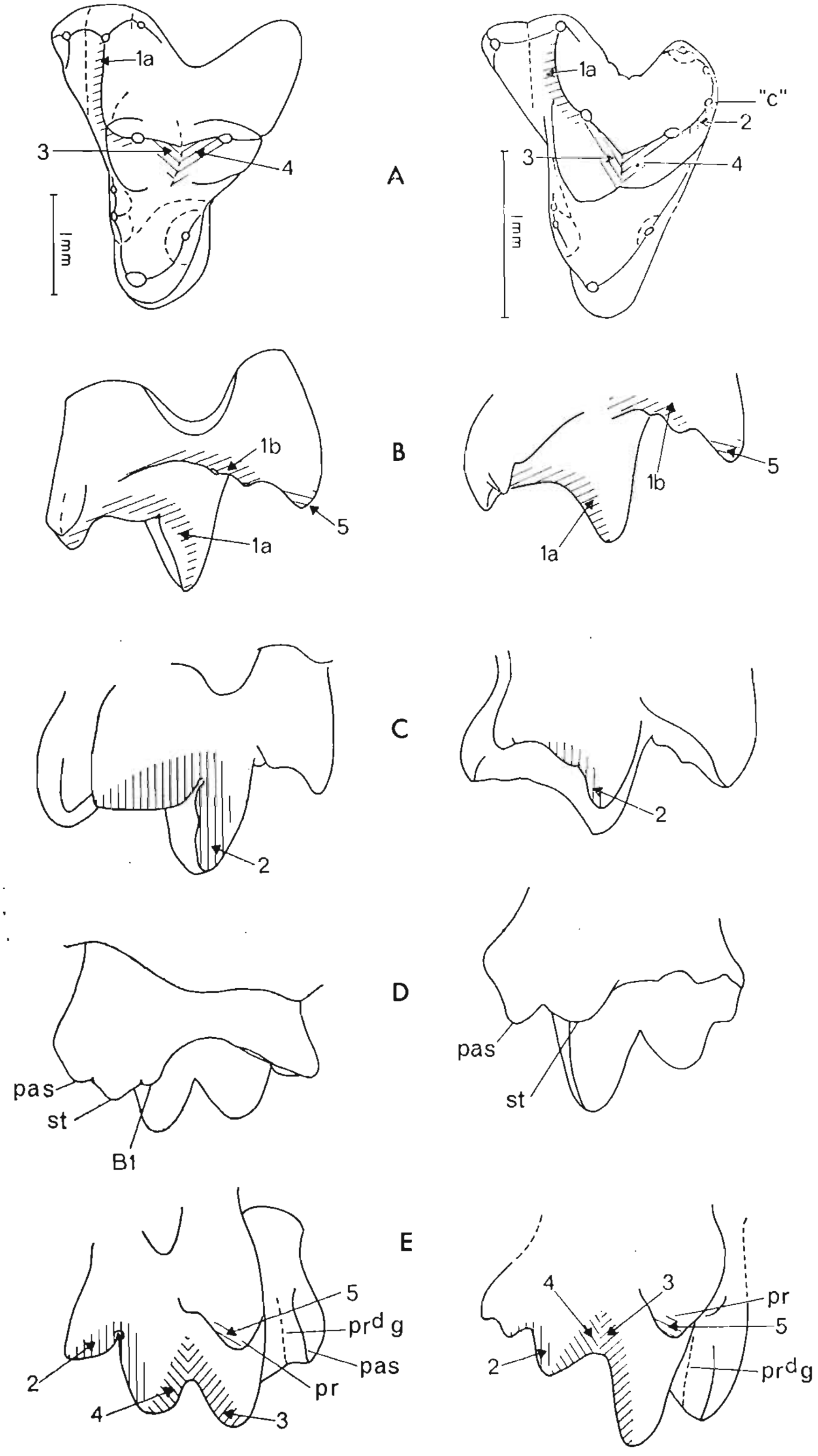


Fig. 8
Comparison of M² of *Deltatheridium pretrituberculare tardum* (left) (ZPAL MgM-I/91) and *Pappotherium pattersoni* (right) (SMP-SMU 617225) in *A*, crown, *B*, anterior, *C*, posterior, *D*, external and *E*, internal views. For abbreviation see p. 107.

metaconid. In spite of considerable similarity between the upper molars of *Pappotherium* and *Deltatheridium*, they probably differ slightly in the shearing mechanism and I therefore think it reasonable to leave them for the time being in separate families. The structure of the upper molars in these two genera suggests that they possibly share a common ancestor.

Another genus resembling *Deltatheridium* in certain respects and classified as a therian incertae sedis is *Potamotelses* from the Early Campanian Upper Milk River Formation of Alberta (Fox, 1972). *Potamotelses* upper molar has a large stylar region, the paracone is somewhat larger than the metacone and it is placed slightly more lingually, the protocone is small and situated at a level far above that of the paracone. The stylar region is proportionally shorter (tr.) than in *Deltatheridium*, especially the metastylar region. In both genera there is only one cusp — metastyle on the metastylar region. The parastylar region is very differently shaped. The parastylar region anterior to the stylocone is wide (tr.), whereas it is narrow in *Potamotelses* (see Fox, 1972, Fig. 1a). In *Deltatheridium* the paracingulum extends from the paraconule along the anterior wall of the tooth to a point above the tip of the paracone, in *Potamotelses* only a possible remnant of the paracingulum can be recognised above the paracone tip and conules are lacking. The ectoflexus is less strongly incurved in *Potamotelses* than in *Deltatheridium*, and the crenulations along its margin are larger in *Potamotelses* than in *Deltatheridium*. The metacrista is much shorter in *Potamotelses* than in *Deltatheridium* and Fox claims that a cusp "c" (Crompton, 1971) is present in *Potamotelses*, while in *Deltatheridium* a carnassial notch is present in the metacrista. The protocone is very differently shaped in the two genera, it is narrow (tr.) and pointed in *Deltatheridium*, while in *Potamotelses* it is not pointed and the protofossa is wider (tr.) and less basined. In both *Potamotelses* and *Deltatheridium* precingula and postcingula are absent. The lower molars of *Potamotelses* resemble those of *Deltatheridium* in having the paracone larger than the metacone and distinctly separated. However, the trigonid is taller and narrower in *Deltatheridium* than in *Potamotelses*. The posterior wall of trigonid has a different structure in the two genera. In *Potamotelses* there is a distinct groove in the external surface of the metaconid; this clearly separates the two shearing surfaces: on the posterior wall of the protoconid (surface 1) and metaconid (surface 5). In *Deltatheridium* this groove is absent and only a slight ridge separates the two shearing surfaces, as is the case in most Cretaceous mammals with tribosphenic dentition. In *Potamotelses* the marked shearing surface 1 is confined to the protoconid and surface 5 to the metaconid, whereas in *Deltatheridium* the shearing surface 1 is present on both the protoconid and part of the metaconid, while the shearing surface 5 is small and extends only along the lingual part of the posterior wall of the metaconid. In other words, the typical "trapshear mechanism" (Crompton, 1974), well developed in *Deltatheridium*, is not present in *Potamotelses*.

The carnassial notches present in *Deltatheridium* on the protocrista and metacrista, as well as on the paracristid, are absent from *Potamotelses*. The talonid in *Potamotelses* has a structure very different from that of *Deltatheridium*, it is wide (tr.) with three or four well developed talonid cusps, while in *Deltatheridium* the talonid is very narrow and trigonid cusps very poorly developed. The above comparison of the structure of the molars of *Deltatheridium* and *Potamotelses*, as well as the analysis of the shearing surfaces in *Deltatheridium* published in this paper, show that the two genera differ markedly. *Deltatheridium* has well developed shearing surfaces along both anterior and posterior walls of the upper molars, shearing surface 2 being larger than the shearing surface 1, whereas in *Potamotelses* (based on the upper tooth) the shearing surfaces are not as well developed. In *Deltatheridium* the entocristid is very low, the protocone tip is exposed lingually when the teeth are in centric occlusion (Text-fig. 6*A*), and the shearing surface 6 is not present, whereas in *Potamotelses*, in which the talonid basin is very large, the protocone tip is not visible lingually when the teeth are in centric occlusion because of the high lingual wall of the talonid, and the shearing surface 6 is very well developed. The above comparison shows that, in spite of the apparent similarity between the molars of *Potamotelses* and *Deltatheridium*, they differ basically in many points and the analysis of their occlusion shows that they functioned in quite different ways. The conclusion is that *Deltatheridium* and *Potamotelses* are not closely related and belong to different groups of mammals, *Deltatheridium* representing a primitive type of molar occlusion, *Potamotelses* a strongly advanced one.

Fox (1972) compared *Potamotelses* with *Aegialodon* (K. A. Kermack *et al.*, 1965) and claimed a great similarity between the lower molars of these genera. However, on the posterior wall of the trigonid surface in *Aegialodon* (K. A. Kermack *et al. l. c.* Fig. 9) there are three shearing surfaces, whereas only two in *Potamotelses*. I do not recognise the floor of the groove, separating the posterior surfaces of the protoconid and metaconid in *Potamotelses*, as being homologous to the shearing surface "d" described by K. A. Kermack *et al.* (1965) for *Aegialodon* and present on the posterior surface of the metaconid. It appears from the analysis of the type of shearing surfaces in *Aegialodon* and a reconstruction of the upper molars in this genus done by Crompton (1971) that the separate middle shearing surface (surface "d" of K. A. Kermack *et al.*, 1965) was probably caused by the protoconule, which was not aligned with the paracrista, and that the paracingulum extending from the protoconule labially was rather well developed. As the shearing surface 1b (lead by paracingulum) on the upper molar was probably arranged at a different angle than the shearing surface 1a (lead by paracrista), the matching shearing surfaces on the trigonid have to be arranged also at different angles to each other. Thus it is very probable that in *Aegialodon*, which is regarded by Fox (1972) as close to the ancestors of *Potamotelses*, the paracingulum and paraconule were probably developed.

COMPARISON OF THE DELTATHERIDIIDAE WITH THE MARSUPIALS

The fragments of skull of *Deltatheridium*, which are preserved, show striking similarities to those of primitive marsupials, such as, e.g., *Didelphis*. The similarities are in the structure of the nasals, which are expanded posteriorly and contact the lacrimals; in details of the structure of the lacrimal, which in both groups has a very large facial wing and the lacrimal foramen situated in the same position; and in the structure of the zygomatic arch, which in both groups is deep, with the jugal extending far anteriorly to a level opposite the anterior margin of the lacrimal and posteriorly as far as the glenoid fossa. The characters which the Deltatheridiidae and primitive marsupials have in common are primitive features and some of them (e.g. expanded nasals and long jugal) also occur in the Late Cretaceous eutherian mammals from Asia (Kielan-Jaworowska, 1969 and 1975). However, the Deltatheridiidae are in the structure of the snout closer to the primitive marsupials than the Cretaceous eutherian mammals from Asia. *Deltatheridium* differs from most marsupials in lacking palatal vacuities; however, the modern marsupial genus *Philander* from Panama has no palatal vacuities and the structure of the palate is similar to that of *Deltatheridium*. The Deltatheridiidae have a metatherian dental formula, but it is possible that the primitive therians had four molars, the last one being lost in eutherians. If this is correct, then the metatherian dental formula in the Deltatheridiidae, with a tendency towards the loss of the last molar, would not necessarily imply that they are marsupials. The structure of the molars of the Deltatheridiidae is different from that of most of the American Cretaceous marsupials (Clemens, 1966;

SLAUGHTER, 1968*b*; LILLEGRAVEN, 1969; SAHNI, 1972; SIGÉ, 1973). Also, the early Cretaceous forms such as *Holoclemensia* differ from the Deltatheridiidae in possessing a mesostyle (absent in Deltatheridiidae) and in having a parastylar region which is much larger than the metastylar region. The lower molars have not been found in occlusion with the uppers of *Holoclemensia;* however, lower molars that have been assigned to *Holoclemensia* by SLAUGHTER (1971) differ from those of the Deltatheridiidae in having the paraconid smaller than the metaconid and the entoconid twinned with hypoconulid. TURNBULL (1971) assigned to *Holoclemensia* two different types of lower molars, but these are clearly not from congeneric forms. In one of these types, represented, e.g., by the specimen PM 1005 in the Field Museum collection (TURNBULL, 1971, Fig. 5c), the paraconid is very small, smaller than the metaconid, whereas in the other type represented, e.g., by the specimen PM 965 from the same collection (TURNBULL, *l. c.* Fig. 4, middle row, second figure from the top) the paraconid is larger than the metaconid, as is the case in the Deltatheridiidae. It follows, therefore, that the identification of isolated lower teeth as belonging to the genus *Holoclemensia* is doubtful.

Of the Cretaceous marsupials only the Stagodontidae are in some respects similar to the Deltatheridiidae; for example, in both the paraconid is larger than the metaconid. However, in the Stagodontidae the entoconid and hypoconulid are twinned, as in all primitive marsupials, which is not the case in the Deltatheridiidae. The talonid is narrow (tr.) in the Deltatheridiidae, but comparatively wide in the Stagodontidae. The upper molars in both groups show some resemblance in that they lack a stylar cusp C, but the general pattern of the upper molars is different; the stylar shelf in the Stagodontidae is not as wide (tr.) as in the Deltatheridiidae; the conules in the Stagodontidae are winged (CLEMENS, 1966; FOX, 1971) and the paracingulum in the Stagodontidae is more extensive than in the Deltatheridiidae; the paracone in the Stagodontidae is smaller than the metacone, while the reverse is the case for the Deltatheridiidae.

COMPARISON OF THE DELTATHERIDIIDAE WITH EUTHERIAN MAMMALS OF THE LATE CRETACEOUS OF ASIA

The known therian fauna from the Late Cretaceous of Asia contains seven monotypic genera (see Table 2). Four of these genera: *Kennalestes*, *Asioryctes*, *Zalambdalestes* and *Barunlestes* are regarded as true eutherians and they are assigned to the three families: ?Leptictidae, Palaeoryctidae and Zalambdalestidae (KIELAN-JAWOROWSKA, 1969 and 1975).

Hyotheridium from the Djadokhta Formation is known from a single specimen (AMNH 21702) which is so badly damaged that only a few features can be recognised. For this reason *Hyotheridium* cannot be assigned to a specific family. However, it should be stressed that the strong, single rooted canines and the short snout of *Hyotheridium* are much more reminiscent of the Deltatheridiidae than of the true eutherian mammals from the same formation. Because of the paucity of the material I shall not discuss *Hyotheridium* further.

All the eutherian genera listed above from the Late Cretaceous of Asia are highly specialised in different directions (and assigned to three different families), but despite of this have many features in common, which suggest that they have derived from a common ancestor; these features differentiate them from the Deltatheridiidae. Deltatheridiidae are characterised by a short snout (which suggests a carnivorous specialisation), nasals which are expanded posteriorly to contact the lacrimals, lacrimal large with an extensive facial wing, large lacrimal foramen and zygomatic arches strong and deep, with jugal reaching far backwards. The

Table 2

The Late Cretaceous therian fauna of Asia

Infraclass	Family	Species	
		Djadokhta Formation (? Santonian)	Barun Goyot Formation and Khermeen Tsav formation (? Middle Campanian)
Eutheria	? Leptictidae	*Kennalestes gobiensis*	
	Palaeoryctidae		*Asioryctes nemegetensis*
	Zalambdalestidae	*Zalambdalestes lechei*	*Barunlestes butleri*
Theria of metatherian-eutherian grade	Deltatheridiidae	*Deltatheroides cretacicus* *Deltatheridium pretrituberculare pretrituberculare*	*Deltatheridium pretrituberculare tardum*
	Uncertain family	*Hyotheridium dobsoni*	

eutherian mammals listed above are in contradistinction characterised by: slender, strongly elongated snouts (especially so in *Zalambdalestes*), posteriorly expanded nasals, which probably contact the lacrimals, comparatively large lacrimals, although they are relatively smaller than in the Deltatheridiidae and have smaller lacrimal foramina. In these eutherian mammals the zygomatic arches are very slender, the jugal is less deep than in the Deltatheridiidae, but reaches far backwards.

Both the Deltatheridiidae and the eutherian mammals have more than three upper incisors. There are probably four in the Deltatheridiidae, probably four in *Kennalestes*, five in *Asioryctes* and possibly three in the Zalambdalestidae. The number of lower incisors is reduced in the Deltatheridiidae to two or one, while in *Kennalestes* there are probably three or more lower incisors, four in *Asioryctes* and three (the first one unusually enlarged) in the Zalambdalestidae.

The maxillary dentition is quite different in the Deltatheridiidae and in the Asiatic Cretaceous eutherian mammals. In the Deltatheridiidae there is a strong, single-rooted canine, followed by three non-molarized premolars and three to four molars, whereas in the here discussed eutherian mammals the canine is strong but double-rooted and situated some distance to the rear of the premaxillo-maxillary suture. The only exception is *Barunlestes*, which was probably derived from *Zalambdalestes* and which has a single-rooted upper canine. It should be noted that in *Kennalestes* the deciduous upper canine is also single-rooted and it is only the permanent one which is double-rooted. The double-rooted canine in these eutherian mammals is separated from a small P^1 by a narrow space, both P^1 and P^2 are double-rooted and do not come into occlusion with the lower premolars. The strongest tooth in the whole series is P^3, with a high, piercing paracone. In the Zalambdalestidae P^3 has a strongly developed protocone, while in *Kennalestes* and *Asioryctes* there is an incipient protocone. P^4 is semi-molariform in all the listed eutherian genera. In the Zalambdalestidae it is strongly elongated transversely, the protocone is well developed and only an incipient metacone is present as a cuspule on the metacrista. In *Kennalestes* and in *Asioryctes* P^4 shows a more advanced degree of molarization, the protocone is developed as in the molars and an incipient metacone, which is smaller than that of the molars, is present. As far as the lower dentition is concerned, the lower incisors, although differently developed in various genera discussed here, are in all cases semi-procumbent; the lower canine is in *Kennalestes* and *Asioryctes* double-rooted, while it is single-rooted in the Zalambdalestidae, the two first premolars are in all the genera comparatively short, third and fourth lower premolars are tall piercing teeth, P_4 is semi-molariform in the Zalambdalestidae, but not so in *Kennalestes* or in *Asioryctes.*

The above comparison shows that all the Late Cretaceous Asian eutherian mammals are similar to one another in the general appearance and organisation of the dentition when seen in lateral view (Kielan-Jaworowska, 1975, figs 1 and 2) and differ from the Deltatheridiidae.

It is difficult to draw any conclusion as to the homology of the teeth in the Asiatic eutherian mammals and the Deltatheridiidae. As stated above, in the Deltatheridiidae the upper canine is strong and single-rooted, while in the Late Cretaceous Asiatic eutherian mammals it is with one exception double-rooted, situated some distance behind the premaxillo-maxillary suture. Single-rooted, strong canines are a feature of primitive (Triassic and Jurassic) mammals and of the cynodonts (SIMPSON, 1928; PARRINGTON, 1971; MILLS, 1971; CROMPTON, 1974). The possibility exists that the double-rooted tooth, designated as an upper canine in the Asiatic Cretaceous eutherians, is not homologous with the single-rooted canine of the Deltatheridiidae and of the Triassic mammals and cynodonts, but represents the first premolar, the primitive canine presumably having been lost. This would possibly explain why there is always a space between the premaxillo-maxillary suture and the double-rooted canine of the Asiatic eutherians. In *Asioryctes,* which has five upper incisors (KIELAN-JAWOROWSKA, 1975), the last incisor is situated just within the premaxillo-maxillary suture and it is possible that this tooth is a reduced canine rather than an incisor. If this hypothesis is correct, there are five upper premolars and three molars in the eutherian genera being discussed, the first premolar acting as a canine and showing a tendency in evolution to the replaced by the reduced, single-rooted tooth.

Whether we accept the first maxillary tooth in the Late Cretaceous eutherian mammals as the true canine, homologous to that of the Deltatheridiidae, or as the first premolar, the general organization of the dentition of the Deltatheridiidae and the Asiatic eutherian mammals is quite different. The differences in the skull and teeth structure between the Deltatheridiidae and the Late Cretaceous Asiatic eutherians show that these groups are not very closely related and, if they have derived from a common ancestor, the divergence took place long ago before the Late Cretaceous, presumably at the beginning of the Early Cretaceous.

It follows that the Deltatheridiidae are in the general organization of the dentition and in the coronal structure of the molars different from undoubted eutherian and metatherian mammals. They probably represent a third, separate evolutionary line, (what has been also suggested by LILLEGRAVEN, 1974) and are therefore classified as Theria of metatherian-eutherian grade.

Among the Asian eutherian mammals I do not know any forms which could be with certainty recognised as possible descendants of the Deltatheridiidae. However, certain North American Paleocene Palaeoryctidae, such as *Didelphodus* have upper molars strikingly similar to those of *Deltatheridium,* but this is not true for all North American Palaeoryctidae. However, this must not be taken to imply that some of the North American Palaeoryctidae are the descendants of Asiatic Deltatheridiidae especially in view of the fact theat the Palaeoryctydiae have a eutherian dental formula. It appears that the forms at present classified as the Palaeoryctidae are not a homogeneous group, and should be revised.

Polska Akademia Nauk
Zakład Paleoozologii,
02-089 Warszawa, Al. Żwirki i Wigury 93
January, 1974

ADDENDUM

When this paper was submitted to publication, a paper by Fox (1974) appeared, in which he describes a single upper molariform tooth from the upper part of the Edmonton Formation, a single lower molar and a lower molar trigonid from the Lance Formation and a lower molar talonid from the Oldman Formation, which show strong similarities to the Asian Deltatheridiidae. On this basis Fox claims that the Deltatheridiidae occured in the Late Cretaceous of North-America. Although I agree that the similarities between these teeth and those of the Deltatheridiidae are striking, I think that the occurrence of the Deltatheridiidae in North America cannot be regarded as proven, as we do not know the dental formulae of the animals to which these teeth belong, and the similarities in the structure of isolated teeth may be due to convergence.

REFERENCES

ARCHER, M. 1972. The development of the cheek teeth in Antechinus flavipes (Marsupialia, Dasyuridae). — *Australian Mammalogy*, **1**, 68.

BELIAJEVA, E. I. — see БЕЛЯЕВА, E. И.

BENSLEY, A. B. 1906. The homologies of the stylar cusps in the upper molars of the Didelphidae. — *Univ. Toronto Stud. Biol. Ser.*, **5**, 149-159, Toronto.

BUTLER, P. M. 1946. The evolution of carnassial dentition in the Mammalia. — *Proc. Zool. Soc.*, **116**, 2, 198-220, London.

— & KIELAN-JAWOROWSKA, Z. 1973. Is Deltatheridium a marsupial? — *Nature*, **245**, 105-106, London.

CLEMENS, W. A. Jr. 1966. Fossil mammals of the type Lance Formation Wyoming. Part II. Marsupialia. — *Univ. Calif. Pubs. Geol. Sci.*, **62**, 1-122, Berkeley.

— & MILLS, J. R. E. 1971. Review of Peramus tenuirostris Owen (Eupantotheria, Mammalia). — *Bull. Brit. Mus. (Nat. Hist.) Geol.*, **20**, 3, 89-113, London.

CROMPTON, A. W. 1971. The origin of the tribosphenic molar. — *In*: Early Mammals, D. M. Kermack & K. A. Kermack (eds.). Suppl. No. 1, *Zool. J. Linn. Soc.*, **50**, 65-87, London.

— 1974. The dentitions and relationships of the Southern African Triassic mammals Erythrotherium parringtoni and Megazostrodon rudnerae. — *Bull. Brit. Mus. (Nat. Hist.) Geol.*, **24**, 7, 397-437, London.

FOX, R. C. 1971. Marsupial mammals from the early Campanian Milk River Formation, Alberta. *In*: Early Mammals, D. M. Kermack & K. A. Kermack (eds.). Suppl. No. 1, *Zool. J. Linn. Soc.*, **50**, 145-164, London.

— 1972. A primitive therian mammal from the Upper Cretaceous of Alberta. — *Canad. J. Earth Scis.*, **9**, 11, 1479-1494.

— 1974. Deltatheroides — like mammals from the Upper Cretaceous of North America. — *Nature*, **249**, 392, London.

GREGORY, W. K. & SIMPSON, G. G. 1926. Cretaceous mammal skulls from Mongolia. — *Amer. Mus. Novit.*, **225**, 1-20, New York.

KERMACK, D. M., KERMACK, K. A. & MUSSETT, F. 1968. The Welsh pantothere Kuehneotherium praecursoris. — *J. Linn. Soc. (Zool.)*, **47**, 312, 407-423, London.

KERMACK, K. A., LEES, P. M. & MUSSETT, F. 1965. Aegialodon dawsoni, a new trituberculosectorial tooth from the Lower Wealden. — *Proc. Roy. Soc., B.*, **162**, 535-554, London.

KIELAN-JAWOROWSKA, Z. 1969. Preliminary data on the upper Cretaceous eutherian mammals from Bayn Dzak, Gobi Desert. — Results Pol. Mong. Pal. Exp. I, *Pal. Pol.*, **19**, 171-191, Pls XXII-XXVII, Warszawa.

— 1974. Multituberculate succession in the late Cretaceous of the Gobi Desert (Mongolia). — Results..., V. *Ibidem*, **30**, 23-44, Pls V-XXI.

— 1975. Preliminary description of two new eutherian genera from the Late Cretaceous of Mongolia. — Results..., VI. *Ibidem*, **33**, 5—15.

— & Barsbold, R. 1972. Narrative of the Polish-Mongolian Palaeontological Expeditions 1967-1972. — Results..., IV. *Ibidem*, **27**, 5-13.

Krebs, B. 1971. Evolution of the mandible and lower dentition in dryolestids (Pantotheria, Mammalia). — *In*: Early Mammals, D. M. Kermack & K. A. Kermack (eds.), Suppl. No. 1, *Zool. J. Linn. Soc.*, **50**, 89-102, London.

Lillegraven, J. A. 1969. Latest Cretaceous mammals of the upper part of the Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. — *Univ. Kans. Paleont. Contr.*, **50**, (Vertebrata 12) 1-122, Lawrence.

— 1974. Biogeographical considerations of the marsupial-placental dichotomy. — *Ann. Rev. Ecol. Syst.*, **5**, 74-95.

McKenna, M. C., Mellett, J. S. & Szalay, F. S. 1971. Relationships of the Cretaceous mammal Deltatheridium. — *J. Pal.*, **45**, 3, 441-442.

Mills, J. R. E. 1964. The dentitions of Peramus and Amphitherium. — *Proc. Linn. Soc. Lond.*, **175**, 2, 117-133, 2 Pls, London.

— 1971. The dentition of Morganucodon. — *In*: Early Mammals, D. M. Kermack & K. A. Kermack (eds.), Suppl. No. 1, *Zool. J. Linn. Soc.*, **50**, 29-63, London.

Parrington, F. R. 1971. On the Upper Triassic mammals. — *Phil. Trans. Roy. Soc. Lond. B.*, **261**, 838, 231-272, London.

Patterson, B. 1956. Early Cretaceous mammals and the evolution of mammalian molar teeth. — *Fieldiana: Geology*, **13**, 1, 1-105, Chicago.

Sahni, A. 1972. The vertebrate fauna of the Judith River Formation, Montana. — *Bull. Amer. Mus. Nat. Hist.*, **147**, 6, 325-412, New York.

Sigé, B. 1973. La faunule de mammifères du Crétacé supérieur de Laguna Umayo (Andes péruviennes). — *Bull. Mus. Nat. Hist. Nat.*, **3**, sér. 99, 375-405, Pls I-II, Paris.

Simpson, G. G. 1928. A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum. — Brit. Mus. (Nat. History), 1-215, London.

Slaughter, B. H. 1965. A therian from the Lower Cretaceous (Albian) of Texas. — *Postilla*, **93**, 1-18, New Haven.

— 1968*a*. Earliest known eutherian mammals and the evolution of premolar occlusion. — *Tex. J. Sci.*, **20**, 1, 3-12, Houston.

— 1968*b*. Earliest known marsupials. —*Science*, **62**, 254-255; Washington.

— 1968*c*. Holoclemensia instead of Clemensia. — *Ibidem*, 162, 1306.

— 1971. Mid-Cretaceous (Albian) therians of the Butler Farm local fauna, Texas. — *In*: Early Mammals, D. M. Kermack & K. A. Kermack (eds.), Suppl. No. 1, *Zool. J. Linn. Soc.*, **50**, 131-143, London.

Szalay, F. S. 1969. Mixodectidae, Microsyopidae, and the insectivore-primate transition. — *Bull. Amer. Mus. Nat. Hist.*, **140**, 4, 195-330, Pls 17-57, New York.

Szalay, F. S. & McKenna, M. C. 1971. Beginning of the age of mammals in Asia: the late Paleocene Gashato Fauna, Mongolia. — *Ibidem*, **144**, 4, 271-317.

Turnbull, W. D. 1971. The Trinity therians: their bearing on evolution of marsupials and other therians. — *In*: Dental Morphology and Evolution, A. A. Dahlberg (ed.), Univ. Chicago Press, 151-179, Chicago.

Trofimov, B. A. see Трофимов, Б. А.

Van Valen, L. 1966. Deltatheridia, a new order of mammals. — *Bull. Amer. Mus. Nat. Hist.*, **132**, 1, 1-126, Pls 8, New York.

Трофимов, Б. А. 1972. Млекопитающие из нижнего мела Монголии. — Сессиа посвященная 100-летию со дня рождения академика А. А. Борисяка, Палеонт. инст. АН СССР, 65-67, Москва.

Беляева, Е. И., Трофимов, Б. А., Рещетов, В. Ю. 1974. Основные этапы эволюции млекопитающих в позднем мезозое-палеогене центральной Азии. — Фауна и биостратиграфия мезозоя и кайнозоя Монголии. — Совм. Сов.-Монг. Палеонм. Эксп. *Труды*, I, 19-45, Москва.

EXPLANATIONS OF PLATES

PLATE XXVIII

Page

Deltatheridium pretrituberculare tardum subsp. n. 108

Upper Cretaceous, Khermeen Tsav formation, Khermeen Tsav II, Gobi Desert, Mongolia

Fig. 1*a*. Part of the rostrum with right and left C-M^3, right canine broken off, ZPAL MgM-I/102, stereo-photograph in anterior view.
Fig. 1*b*. Stereo-photograph of the same in occlusal view.
Fig. 1*c*. Stereo-photograph of the same in dorsal view.
Fig. 1*d*. Stereo-photograph of the same in right lateral view.
Fig. 1*e*. The same in left lateral view.

All × 4

Photo: W. Skarżyński

PLATE XXIX

Page

Deltatheridium pretrituberculare tardum subsp. n. 108

Upper Cretaceous, Barun Goyot Formation, Nemegt, Red monadnocks, Nemegt Basin, Gobi Desert, Mongolia

Fig. 1*a*. Stereo-photograph of the incomplete rostral part of the skull, with strongly damaged cranial roof with left C, P^1 and P^2 and right P^3-M^3, in right lateral view, ZPAL MgM-I/60, × 4.
Fig. 1*b*. Stereo-photograph of the same in occlusal view, × 4.

Photo: W. Skarżyński

Upper Cretaceous, Khermeen Tsav formation, Khermeen Tsav II, Gobi Desert, Mongolia

Fig. 2*a*. Holotype, (young individual), (see also Plates XXX-XXXIV). Stereo-photograph of the left maxilla with broken C, P^1-M^3, ZPAL MgM-I/91, × 6.
Fig. 2*b*. Stereo-photograph of the same in occlusal view, × 6.

Photo: A. Coleman

PLATE XXX

Upper Cretaceous, Khermeen Tsav formation, Khermeen Tsav II, Gobi Desert, Mongolia

Fig. 1*a*. Badly damaged skull, consisting of fragments of the cranial roof and both maxillae, associated with incomplete right and left mandible, before the final preparation in left lateral view, holotype, (see also Plates XXIX and XXXI-XXXIV) ZPAL MgM-I/91, × 6.
Fig. 1*b*. Stereo-photograph of the left mandible, of the same specimen with P_2-M_4, in occlusal view, × 6.
Fig. 1*c*. Stereo-photograph of the right mandible, belonging to the same specimen, with root of single incisor, root of C, roots of P_1 and with P_2-M_2 and roots of M_3 in occlusal view, × 6.

Upper Cretaceous, Barun Goyot Formation, Nemegt, Eastern Sayr, Nemegt Basin, Gobi Desert, Mongolia

Fig. 2*a*. Stereo-photograph of the fragment of the right maxilla with M^1-M^3 in outer view. Left mandible of the same specimen is figured on Pl. XXXV, ZPAL MgM-I/136, × 4.
Fig. 2*b*. Stereo-photograph of the same in occlusal view, × 4.
Fig. 2*c*. Stereo-photograph of the same in inner view, × 4.

Photo: W. Skarżyński and A. Coleman

PLATE XXXI

Upper Cretaceous, Khermeen Tsav formation, Khermeen Tsav II, Gobi Desert, Mongolia

Fig. 1*a*. Stereo-photograph of the right maxilla with damaged P^1 and P^2-M^2 in outer view; holotype (see also Plates XXIX, XXX, XXXII-XXXIV), ZPAL MgM-I/91.
Fig. 1*b*. Stereo-photograph of the same in inner view, showing part of the damaged cranial roof.
Fig. 1*c*. Stereo-photograph of the left mandible of the same specimen with P_2-M_4 in outer view.
Fig. 1*d*. Stereo-photograph of the same in inner view.

All × 6

Photo: A. Coleman

PLATE XXXII

Page

Deltatheridium pretrituberculare tardum subsp. n. 108

Upper Cretaceous, Khermeen Tsav formation, Khermeen Tsav I, Gobi Desert, Mongolia

Fig. 1*a*. Stereo-photograph of the left maxilla with C-M^3 in inner view; holotype (see also Plates XXIX-XXXI, XXXIII and XXXIV), ZPAL MgM-I/91.
Fig. 1*b*. Stereo-photograph of the right maxilla of the same specimen in occlusal view.
Fig. 1*c*. Stereo-photograph of the right mandible of the same specimen with root of a single incisor, broken of canine, broken off P_1, P_2-M_2, roots of M_3, in inner view.
Fig. 1*d*. Stereo-photograph of the same in outer view.

All × 4

Photo: A. Coleman

PLATE XXXIII

Page

Deltatheridium pretrituberculare tardum subsp. n. 108

Upper Cretaceous, Khermeen Tsav formation, Khermeen Tsav I, Gobi Desert, Mongolia

Scanning electron microscope stereo-photographs

Fig. 1*a*. Left M^3 in occlusal view; holotype (see also Plates XXIX-XXXII and XXXIV), ZPAL MgM-I/91.
Fig. 1*b*. The same in inner view.
Fig. 1*c*. Left maxilla of the same with M^1-M^2 in occlusal view.
Fig. 1*d*. The same in inner view.
Fig. 1*e*. The same in anterior view.

All × 11.5

Photo: R. G. Pierce

PLATE XXXIV

Page

Deltatheridium pretrituberculare tardum subsp. n. 108

Upper Cretaceous, Khermeen Tsav formation, Khermeen Tsav I, Gobi Desert, Mongolia

Scanning electron microscope stereo-photographs

Fig. 1*a*. Right M_2-M_3 in oblique anterior view; holotype (see also Plates XXIX-XXXIII), ZPAL MgM-I/91.
Fig. 1*b*. The same in posterior view.
Fig. 1*c*. M_3 of the same in occlusal view.
Fig. 1*d*. M_2 of the same in occlusal view.
Fig. 1*e*. Left maxilla of the same specimen with M^1-M^3 in inner view.

All × 11.5

Photo: R. G. Pierce

PLATE XXXV

Page

Deltatheroides cretacicus GREGORY & SIMPSON 117

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Ruins, Gobi Desert, Mongolia

Fig. 1*a*. Stereo-photograph of the damaged left mandible with fragmentary root of C, roots of P_1, and P_2-M_4 in outer view, ZPAL MgM-I/29, × 4.

Fig. 1*b*. Stereo-photograph of the same in occlusal view, × 4.

Fig. 1*c*. Stereo-photograph of the same in inner view, × 4.

Photo: A. Coleman

Page

Deltatheridium pretrituberculare tardum subsp. n. 108

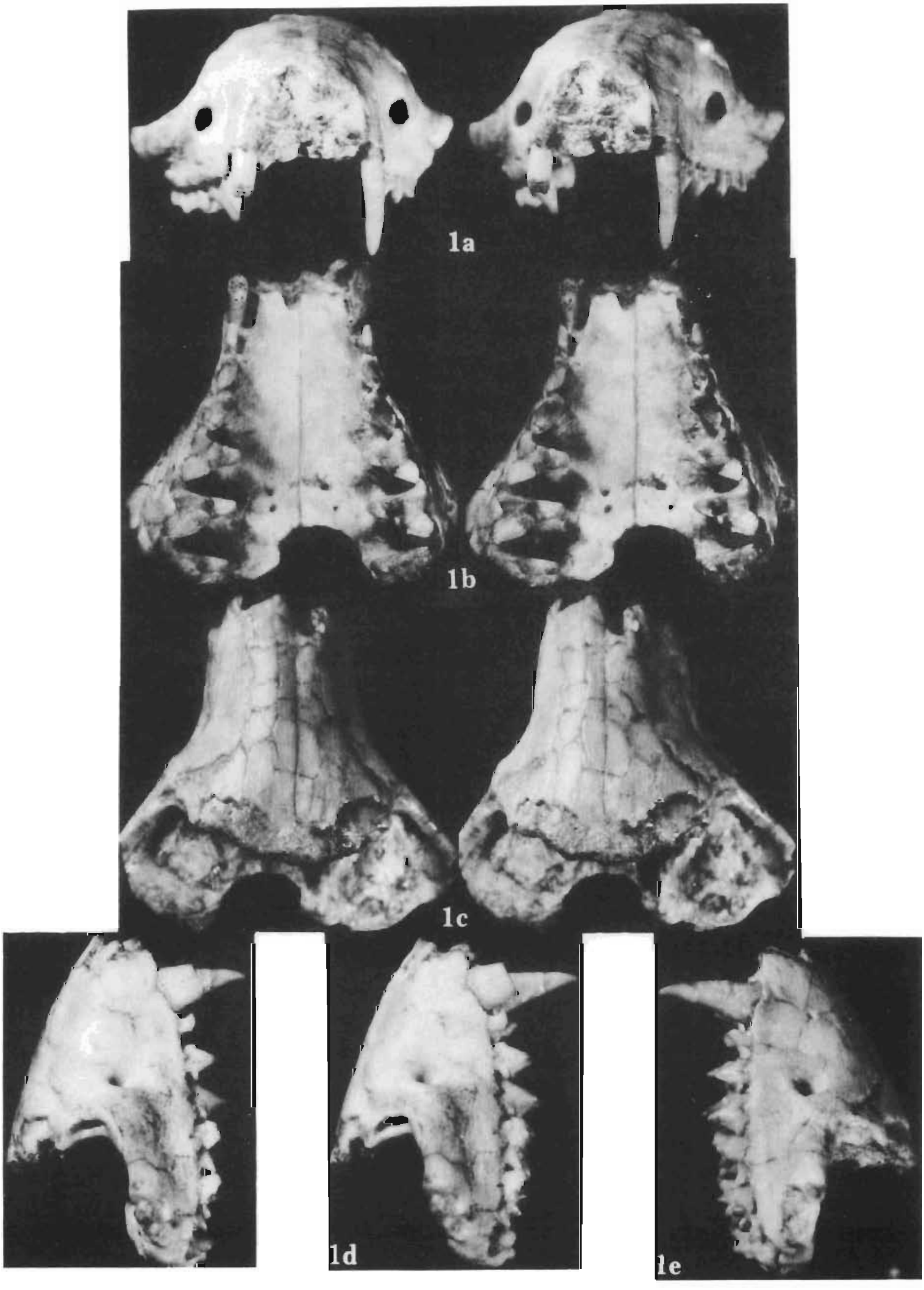
Upper Cretaceous, Barun Goyot Formation, Nemegt, Eastern Sayr, Nemegt Basin, Gobi Desert, Mongolia

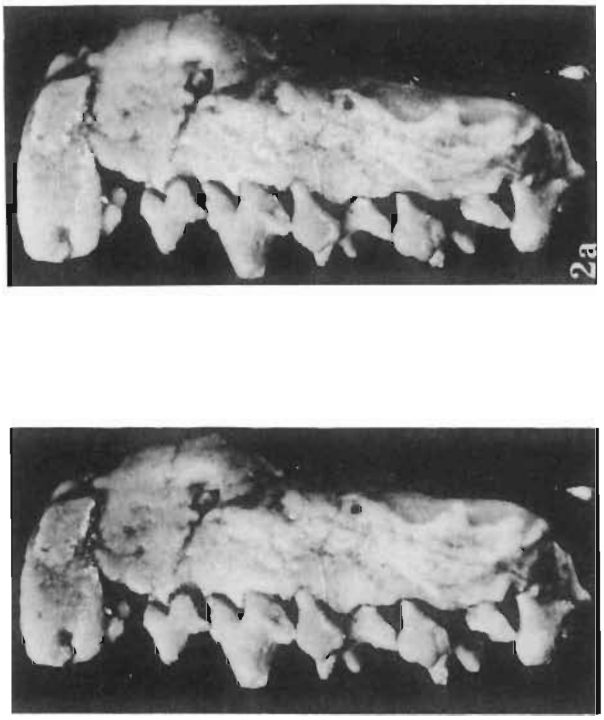
Fig. 2*a*. Stereo-photograph of the fragment of the left mandible with roots of P_4, M_1-M_2 and fragment of root of M_3 in outer view, × 4. Fragment of the right maxilla found in association with this specimen is figured on Plate XXX, ZPAL MgM-I/136.

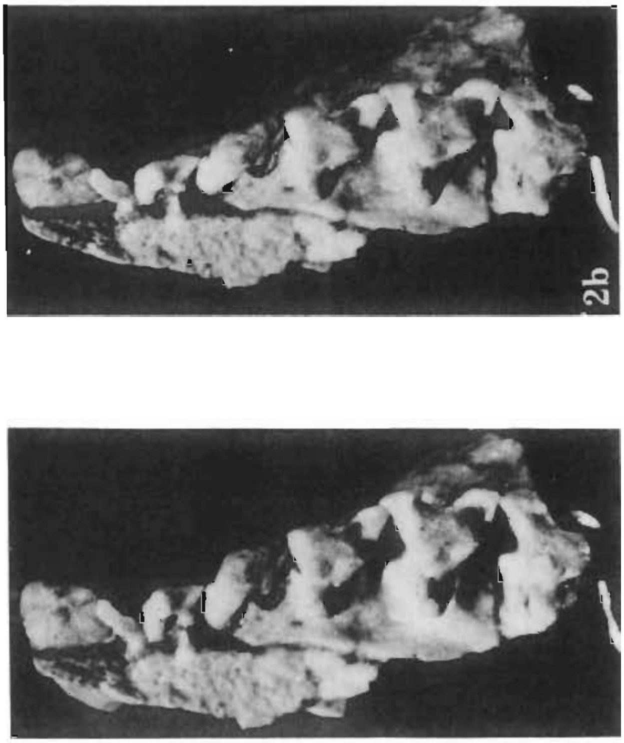
Fig. 2*b*. Stereo-photograph of the same in occlusal view, × 4.

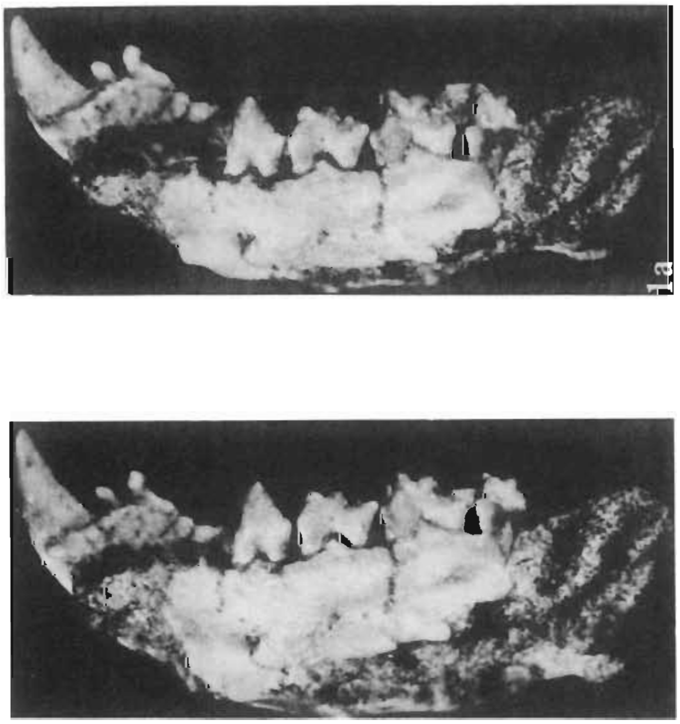
Fig. 2*c*. Stereo-photograph of the same in inner view, × 4.

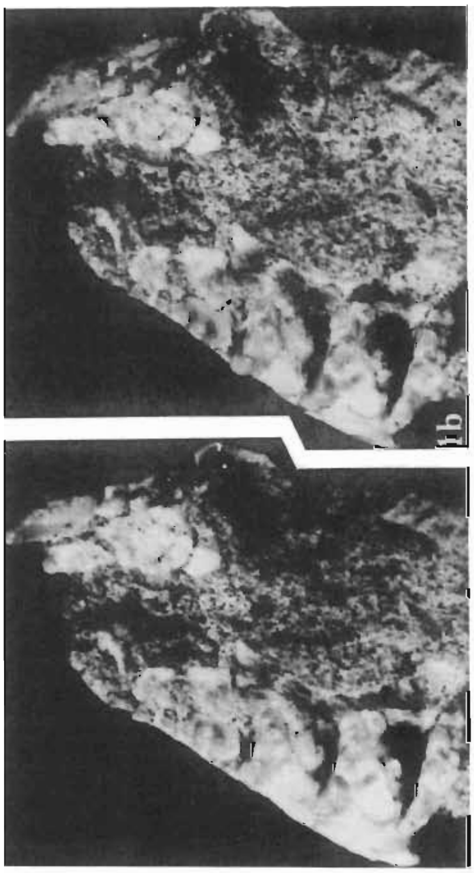
Photo: W. Skarżyński

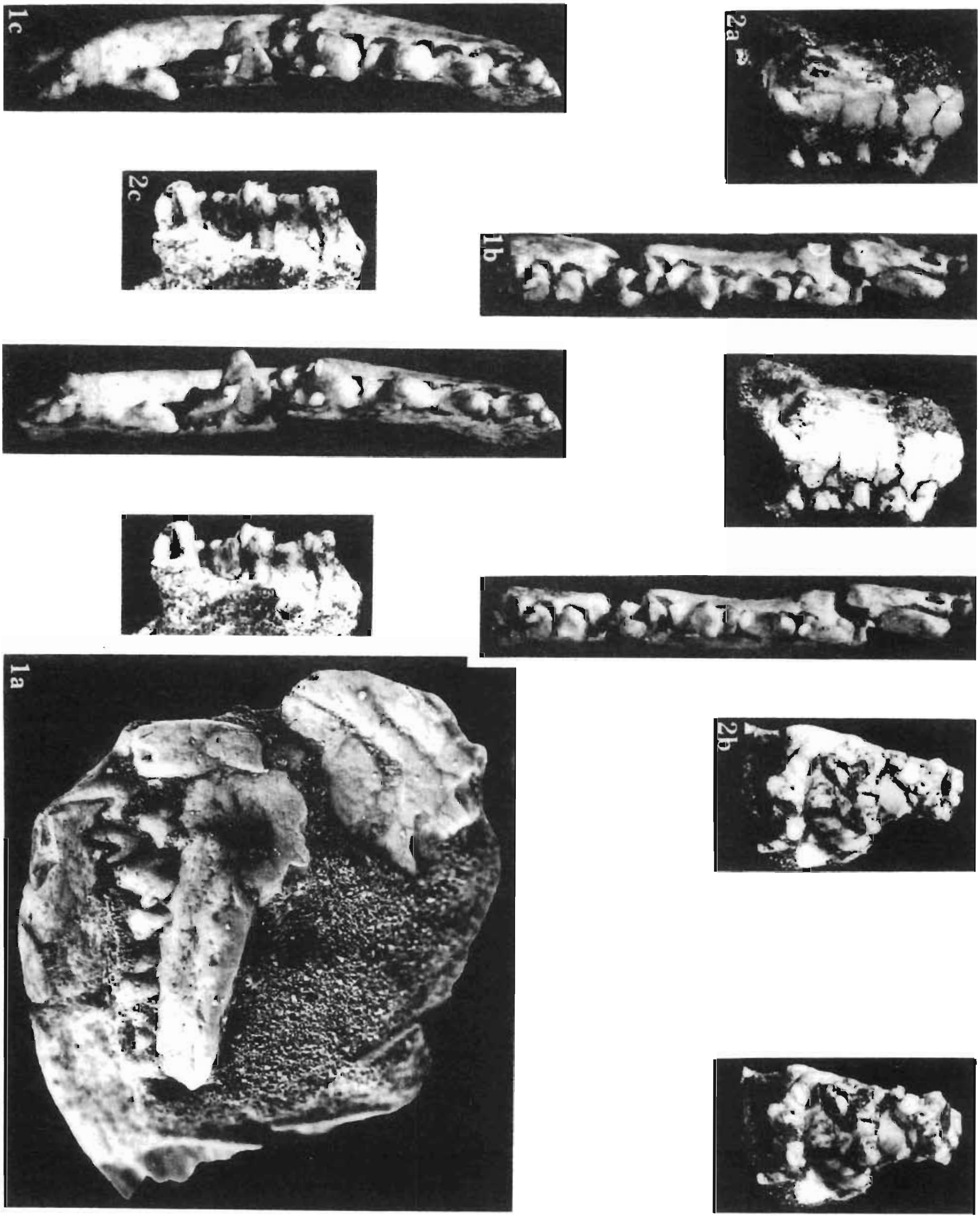

1a
1b
1c
1d
1e

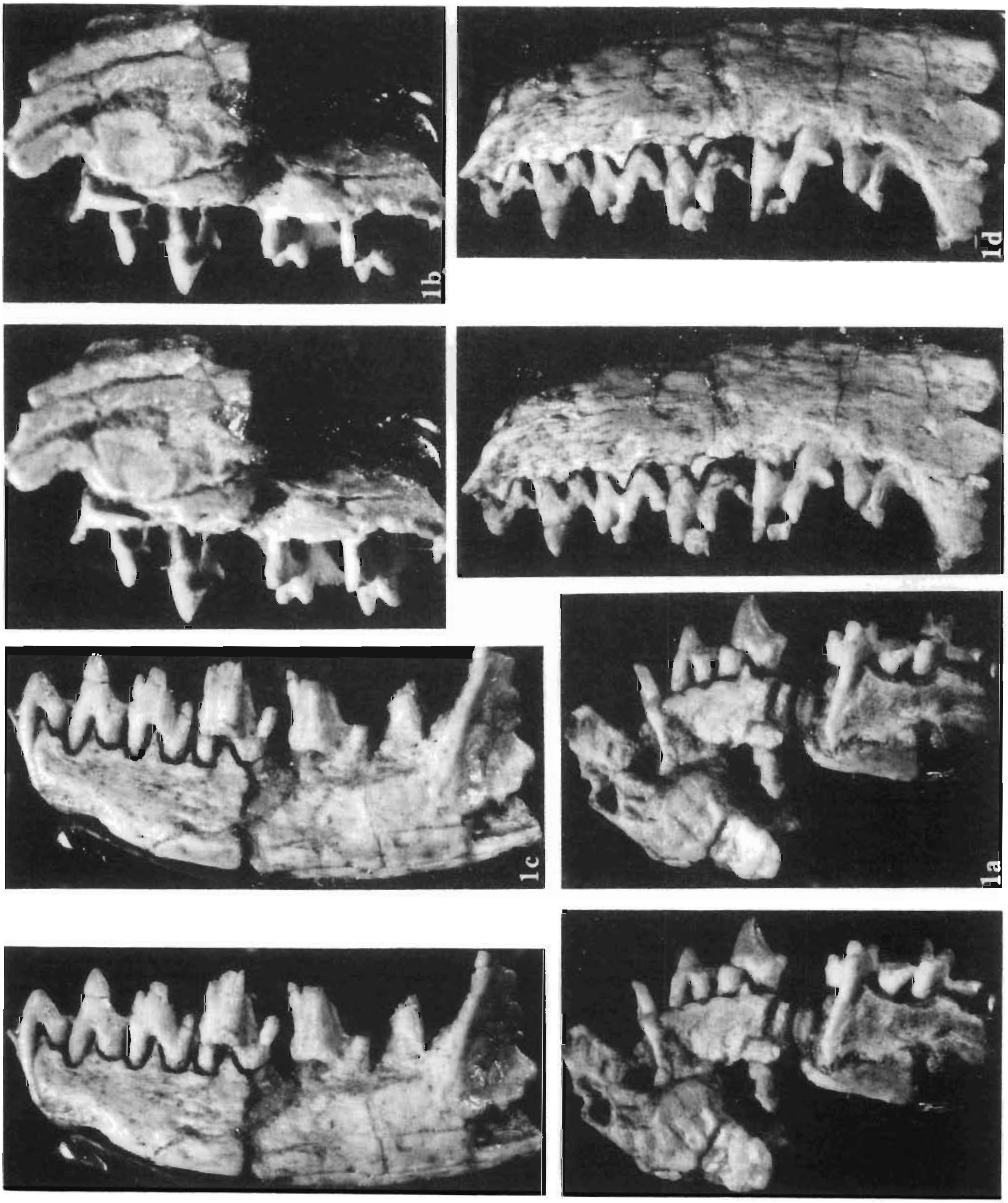

2a

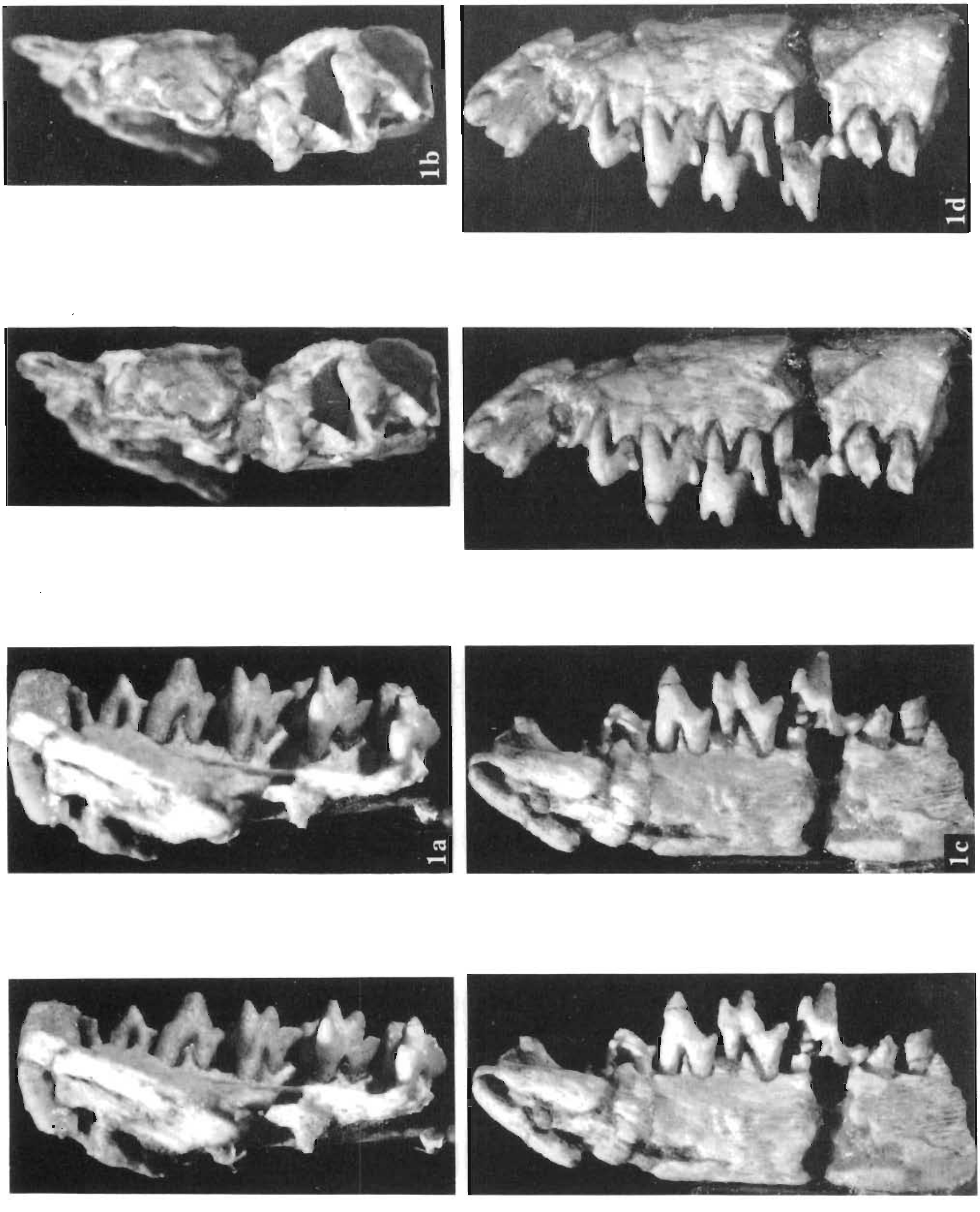

2b

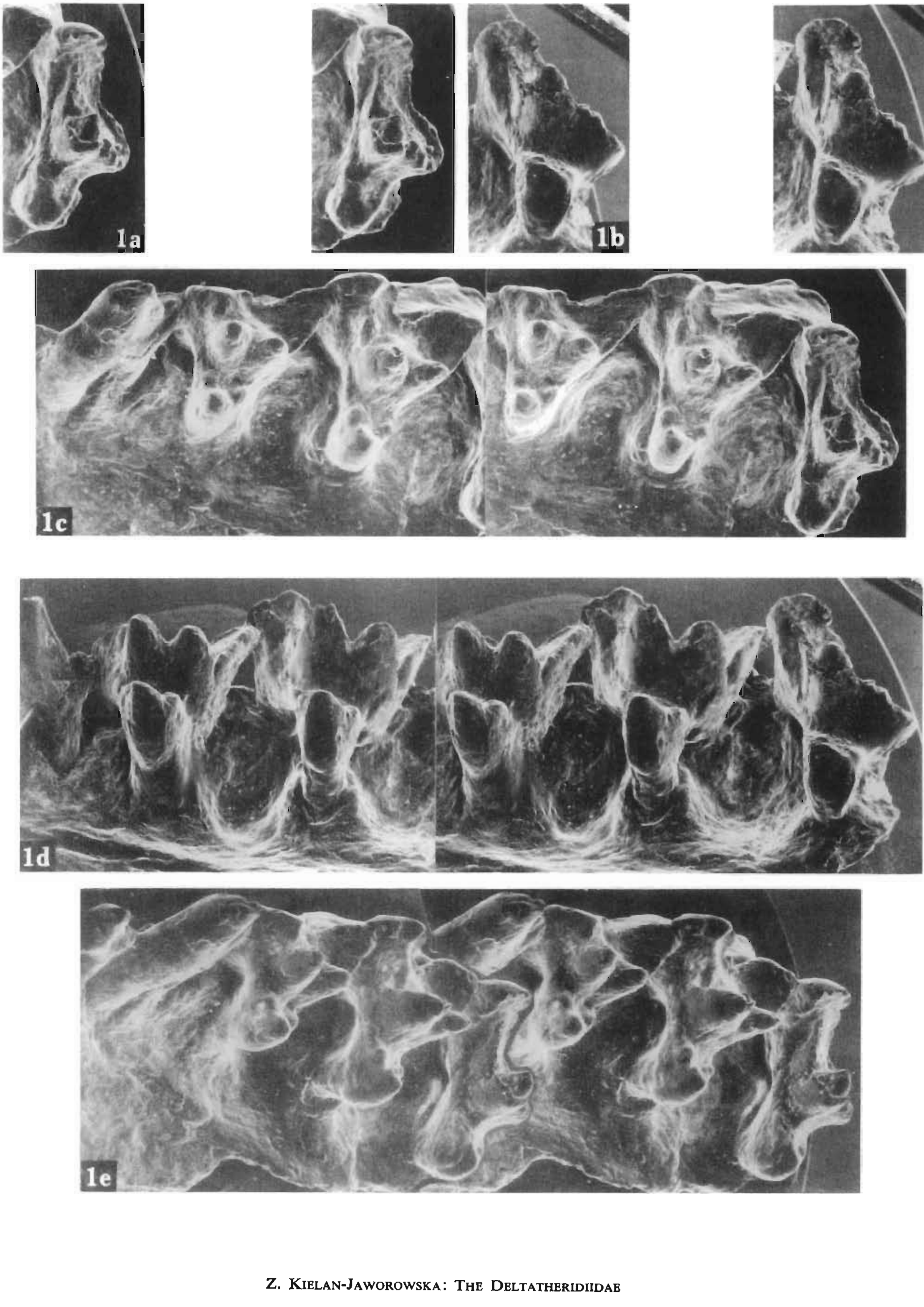

1a

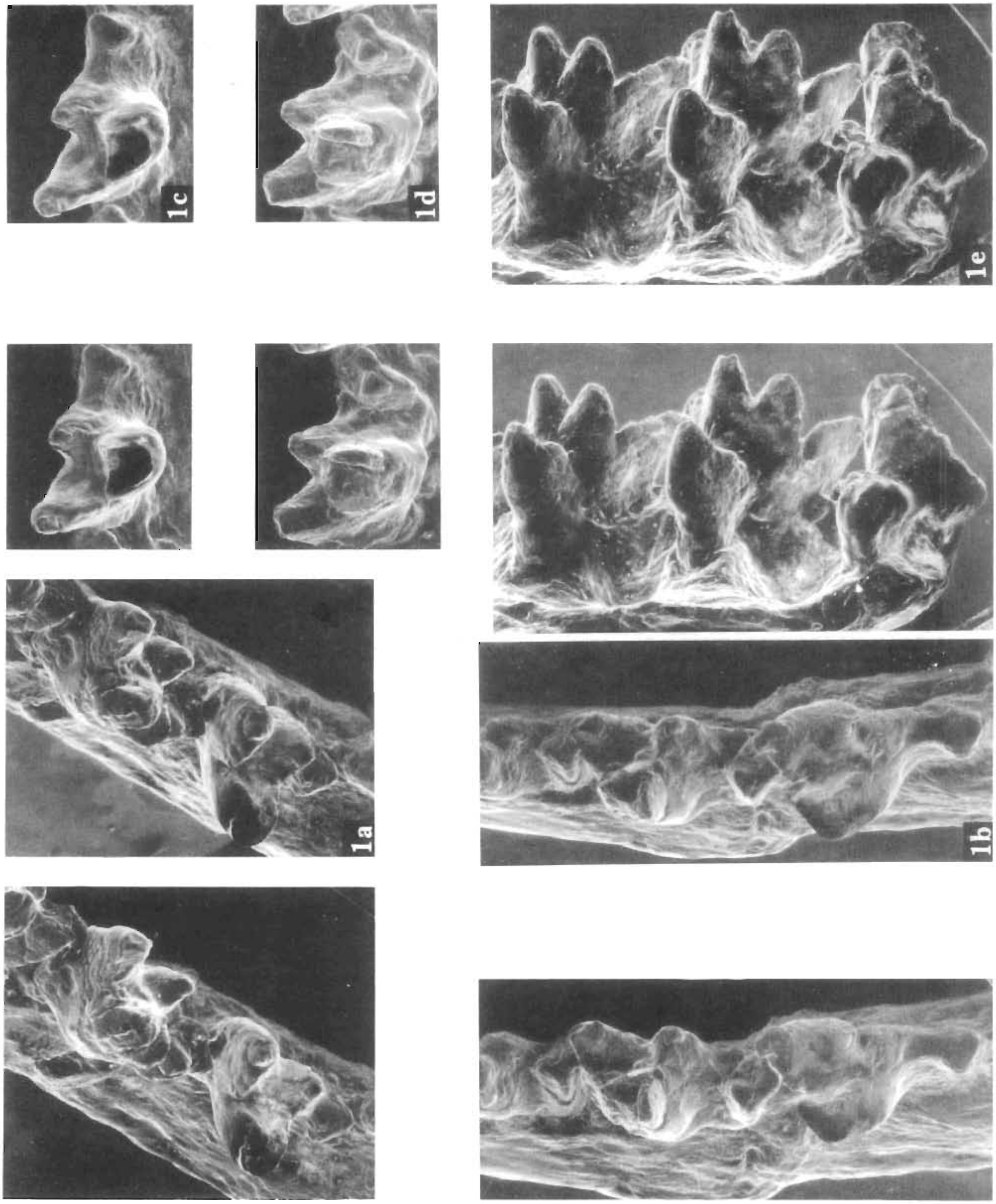

1b

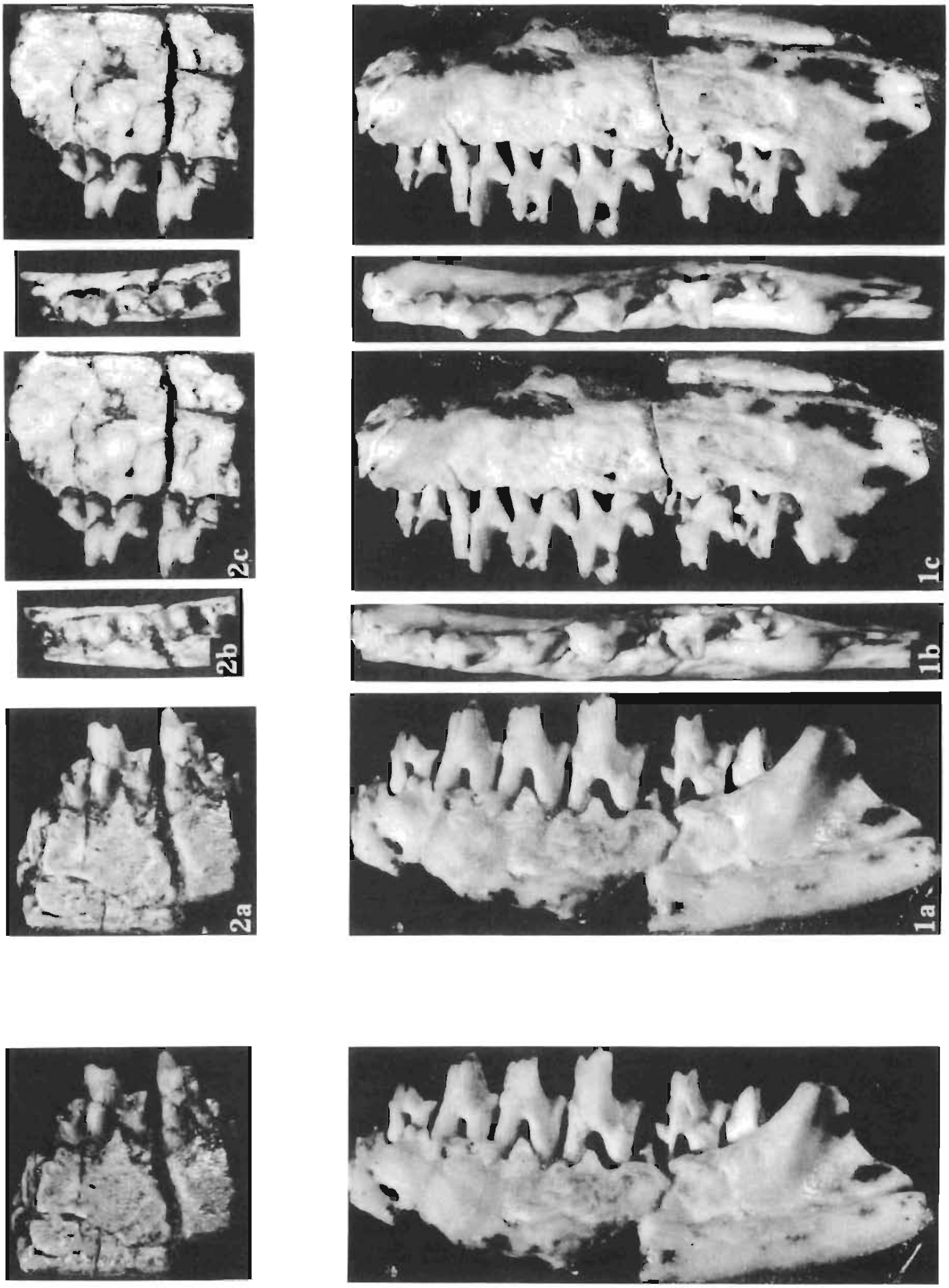

1c
2a
2c
1b
1a
2b


1b
1d
1c
1a


1b
1d
1a
1c


1a
1b
1c
1d
1e


1c
1d
1e
1a
1b


2c
1c
2b
1b
2a
1a